Physiological Ecology of Two Tree Weta Species

A thesis presented in partial fulfilment of the requirements for the degree of

Masters of Science in Zoology

At Massey University, Palmerston North, New Zealand.

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2011

Abstract

Tree weta in New Zealand have been extensively studied for the sexual selection that has resulted in their pronounced sexual dimorphism, yet surprisingly little basic ecological information about common tree weta species is available. Particularly, information on the interactions within and between tree weta species is lacking. As such, this thesis focuses on how tree weta in the North Island of New Zealand are distributed with attention on *Hemideina crassidens* and *H. thoracica* populations and whether or not their distributions are correlated with local temperatures. Using ArcSoft GIS software, I established that while *Hemideina crassidens* have established their populations in colder areas, they do not appear to show greater body size in response to this. Additionally, tree weta from high altitude populations on Mt Taranaki were collected as immature nymphs and raised alongside weta from lowland populations under two temperature treatments. The results indicate that two species of weta from high altitude are more alike in their growth rate than they are to lowland conspecific populations. Mt Taranaki tree weta not only showed fast rates of growth but were larger overall in later instars. Adult weta from Mt Taranaki and lowland populations were also tested for rates of oxygen consumption at various temperatures. Surprisingly, only the temperature at which the weta were tested resulted in metabolic differences, not the population or species differences that were predicted. This information allows more detailed investigations of environment and how changes of local and global climate may affect tree weta distributions.

Acknowledgements

Firstly, thank you to my supervisors, Dr Steve Trewick and Dr Mary Morgan-Richards, for all the enthusiasm, encouragement, wisdom and especially all the tedious proof reading.
Many thanks go to Melissa Griffin, Craig Murray, Shaun Nielsen, Briar Smith, Robyn Dewhurst, Rachel Streeter and Melissa and Aaron Jacobson for all their hard work in the wet, freezing, muddy conditions they faced weta collecting. Melissa and Aaron Jacobson also kindly hosted us on overnight expeditions to Mt Taranaki. Thanks too go to The Department of Conservation for granting me the permit to collect on Mt Taranaki.

Several people have contributed their time and skills to the chapters of this thesis, without which, I would have been lost. So thanks go to Dr Gabe Redding for his advice and software contributing to oxygen metabolism; Matt Irwin for his unending patience and assistance with GIS and Dr Jonathan Godfrey and Penny Bilton, the statisticians who tested my growth rate data for me-something I could not have done myself.

I appreciate and thank Melissa Griffin for her hours of intelligent conversation, companionship in the field and general weta enthusiasm. Thanks also to Dr Cilla Wehi and Dr Mariana Bulgarella for their proof reading and helpful suggestions.

Thank you also to all those within the Ecology Group who have contributed their knowledge, time and expertise: Dr Masha Minor, Dr Ian Henderson, Dr Murray Potter, Tracy Harris, Paul Barrett, Cleland Wallace, Erica Dahya and Jess Costall.

Finally, the biggest thank you goes to my fiancé Craig Murray, who not only accompanied me on weta hunting expeditions and put in some serious time on the weekends in the lab, but supported me with encouragement, endless cups of tea and love. I would also like to thank Craig for the time he took to photograph my unruly subjects and as such, all photographs in this thesis are credited to him.

This thesis was supported by a grant from the Julie Alley Bursary, Massey University.

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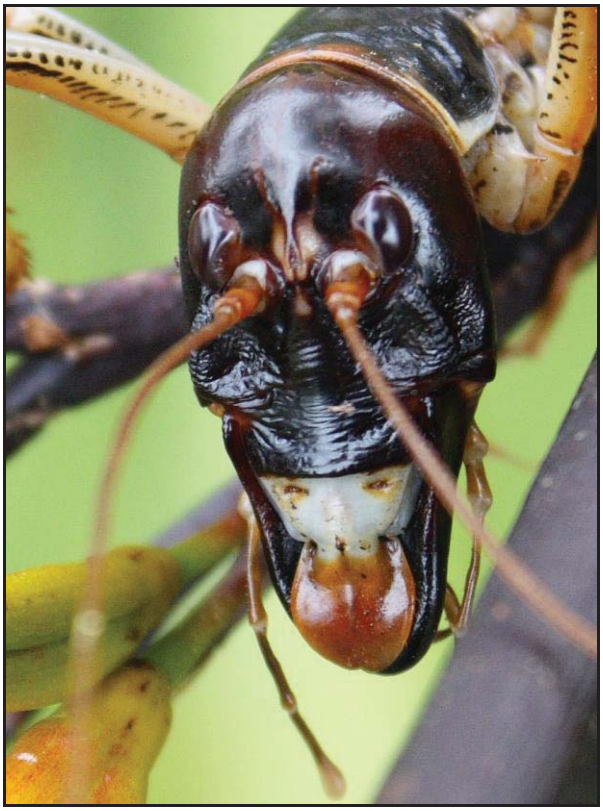


1.1 Competitive exclusion

One can learn a great deal about the ecology of a species by examination of its distribution in relation to closely related species and environmental variables. Two species with similar ecologies are unable to inhabit the same area due to constant conflicts for resources (Reitz & Trumble, 2002). In the case of herbivorous insects, it is not necessarily food resources that are competed for, as in most cases there is an abundance of vegetation, but perhaps living/breeding resources are in short supply. In the case of New Zealand's generalist, herbivorous tree weta, it may be suitable roost holes for males to obtain a harem of females that is the limiting factor (Wehi, unpublished data). This leads two similar species to form a parapatric division where there is very little or no overlap in the distributions of the species (Garcia-Ramos, Sanchez-Garduno, & Maini, 2000). When one species is removed, it can be hypothesised that the remaining species will take advantage of the resources and extend their range. However, when the two species are distributed along a latitudinal or altitudinal gradient, it may be that a combination of competition and environmental variables limit the range of each species (Case, Holt, McPeek, & Keitt, 2005). What are the adaptations in each species that have occurred that prevent range expansion of their competitor? And what environmental parameters limit their range? It is difficult to distinguish the effects of competitive exclusion from adaptations, which leads us to experiment with different species and populations under constant conditions.

1.2 Weta

Order: Orthoptera

Suborder: Ensifera

Superfamily: Stenopalmatoidea (Burmeister 1838)

Family: Anostostomatidae

Subfamily: Deinacridinae

Genus: *Hemideina* (Walker 1869)

Tree weta of the genus *Hemideina* (Walker, 1869) (Ensifera: Anostostomatidae) are nocturnal, flightless orthopterans, endemic to New Zealand and are an iconic group in the New Zealand culture. There are seven recognised tree weta species: *Hemideina crassidens* (Blanchard, Salmon), the Wellington tree weta; *H. thoracica* (White), the Auckland tree weta; *H. trewicki* (Morgan-Richards), the Hawke's Bay tree weta; *H. femorata* (Hutton), the Canterbury tree weta; *H. broughi* (Buller), the west coast bush weta; *H. ricta* (Hutton), the Bank's Peninsula tree weta and *H. maori* (Pictet and Saussure), the alpine tree weta (Gibbs, 2001).

All tree weta are hemimetabolous, so hatch from the egg appearing morphologically like small adults and grow through a series of moults into sexually mature adults. Tree weta are relatively long-lived insects and may take a year to grow to sexual maturity and have an adult life span in the wild of around two years (Kelly, 2008a; McIntyre, 2001). With the exception of *H. broughi*, all *Hemideina* weta are sexually dimorphic (Field & Deans, 2001; Gibbs, 2001; Morgan-Richards & Gibbs, 2001) with males being selected for megalocephaly and wielding heads and mandibles that are up to 40% of the total body length in some species (O'Brien & Field, 2001) allowing the male to successfully defend harems of female weta within prime tree galleries (Gibbs, 2001; Kelly, 2005; Spencer, 1995). Tree weta are unusual in that males may become sexually mature at the eighth, ninth or tenth instar (Field & Deans, 2001; Kelly, 2008b; Spencer, 1995) whilst all females become sexually mature at the tenth instar.

The suborder Ensifera first appears in the fossil record in the carboniferous period (Gorochov, 2001). The large size attained by tree weta (weight >8 g) has been attributed to their evolution in the absence of ground-dwelling mammals (McIntyre, 2001). It is a common misconception that tree weta fill the niche of rodents found in other countries, however, recent studies have shown that not only do tree weta differ significantly in dietary choices from rodents (Griffin, Morgan-Richards, & Trewick, 2011; Griffin, Trewick, Wehi, & Morgan-Richards, 2011), tree weta have not been displaced by the invasion of rodents into New Zealand with the arrival of people and therefore cannot occupy exactly the same niche (Griffin, Trewick, et al., 2011).

Tree weta are likely to have arisen from a common ancestor with *Deinacrida* (giant weta) whose closest extant relative, *Hemideina broughi,* shares a number of ancestral morphological characteristics with both giant and tree weta (Gibbs, 2001) (Figure 1.1). Since the divergence from *Deinacrida*, the tree weta clade has split into two monophyletic groups comprising the North Island species and the South Island species. *Hemideina crassidens*, *H. thoracica* and *H. trewicki* for the northern group whilst *H. maori*, *H. femorata* and *H. ricta* form the southern group (Morgan-Richards & Gibbs, 2001) (Figure 1.1). Despite the fact that *H. crassidens* is found in both the North and South Islands, its position within the phylogeny suggests its origin was in the North Island and has since crossed the Cook Straight to inhabit the South Island. Of the two most widespread North Island species, *H. crassidens* has been the subject of more research than *H. thoracica* (Griffin, Morgan-Richards, et al., 2011; Griffin, Trewick, et al., 2011; Kelly, 2005, 2008b; Morgan-Richards, Trewick, & Wallis, 2000; Trewick & Morgan-Richards, 1995) and the published literature provides an excellent platform from which to explore further these two common species. *Hemideina crassidens* and *H. thoracica* can be distinguished from each other easily in the field by the colouration and striping of the abdomen. *Hemideina crassidens* (Figure 1.2) has an abdomen that is transversely banded in yellow and dark brown dorsally with a usually dark brown pronotum, and *H. thoracica* (Figure 1.2) has a uniformly brown abdomen with lighter, more patterned pronotum.

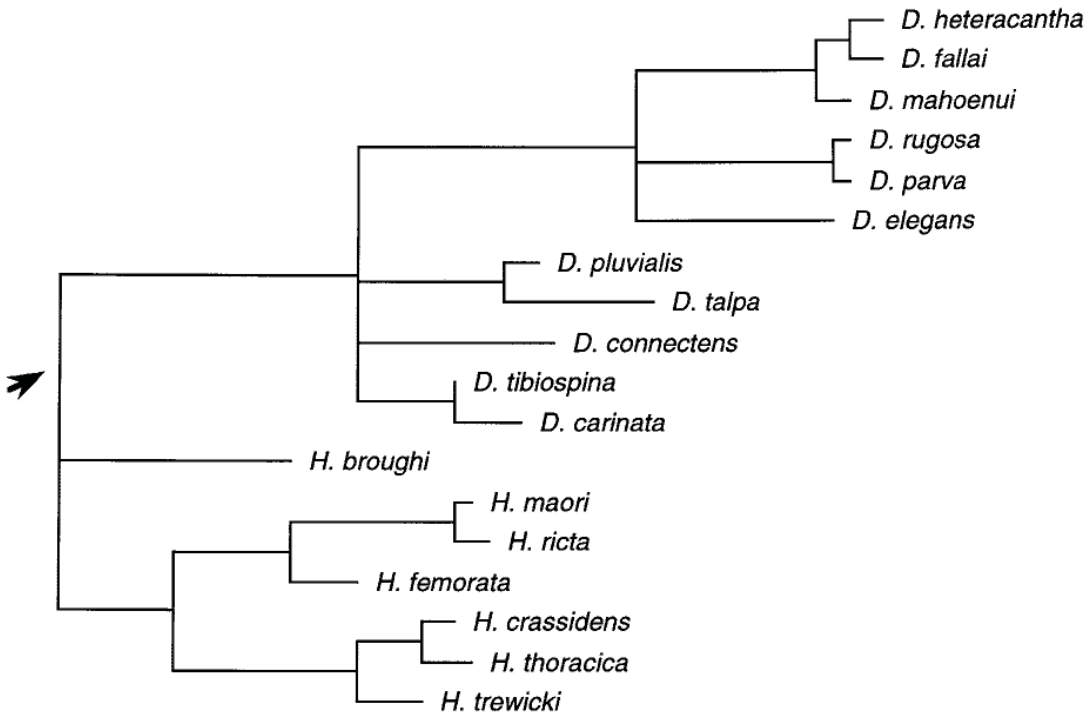


Figure 1.1 A phylogeny of New Zealand *Hemideina* and *Deinacrida* species based on genetic and morphological data, with arrow showing morphological root (Morgan-Richards & Gibbs, 2001).

In the North Island, *Hemideina crassidens*, *H. thoracica* and *H. trewicki* are distributed parapatrically with narrow areas in which they are sympatric where they will share roost cavities (Trewick & Morgan-Richards, 1995). In some of these regions of sympatry individuals that are intermediate in colour pattern have been collected and are considered putative-hybrids (pers obs). Based on chromosome abnormalities and lack of eggs in adult females it is likely these putative-hybrids are infertile (M. Morgan-Richards, personal communication, 12th June 2011). Little is known about the physiological and ecological differences between the two species and this is highlighted on Mount Taranaki where *H. crassidens* and *H. thoracica* form an abrupt distribution junction in the absence of any physical boundaries, with few shared roosts and no putative-hybrids. It appears that these two species are completely reproductively isolated despite no apparent difference from other populations. This thesis seeks to describe differences that distinguish the two species and seeks evidence to support the idea that competitive exclusion is operating between these two species within the North Island. I also seek to determine whether or not *H.*

crassidens and *H. thoracica* on Mt Taranaki show physiological differences to high altitude life compared to lowland populations.

Figure 1.2 *Hemideina crassidens*, tenth instar male (left); *Hemideina thoracica*, tenth instar female (right).

New Zealand's turbulent geological past may play a key role in the isolation of species through parapatric distribution as the shape and climate of New Zealand has undergone massive change. The landscape has been moulded by volcanism, such as the most recent Taupo eruption 1850 years ago (Morgan-Richards, et al., 2000; Wallis & Trewick, 2009); the continual tectonic movements of the alpine fault that continue to form the Southern Alps and the strong impact of the last glacial maximum 22000 years ago (Newnham, et al., 1999). Additionally, anthropogenic deforestation began in 1200AD (McGlone & Wilmshurst, 1999), contributing to habitat loss for tree weta. Any of these events has the capability to maroon populations preventing gene flow and allowing adaptation amongst the relic population in response to a change in environmental factors.

The Maori word "weta" refers generically to all *Hemideina*, *Hemiandrus* and *Deinacrida* and is both the singular and plural form of the noun. For the purpose of this thesis, all 'weta' referred to are *Hemideina* (unless specified) and represent both a singular and plural: in keeping with Maori grammar (Field, 2001).

1.3 Thesis Outline

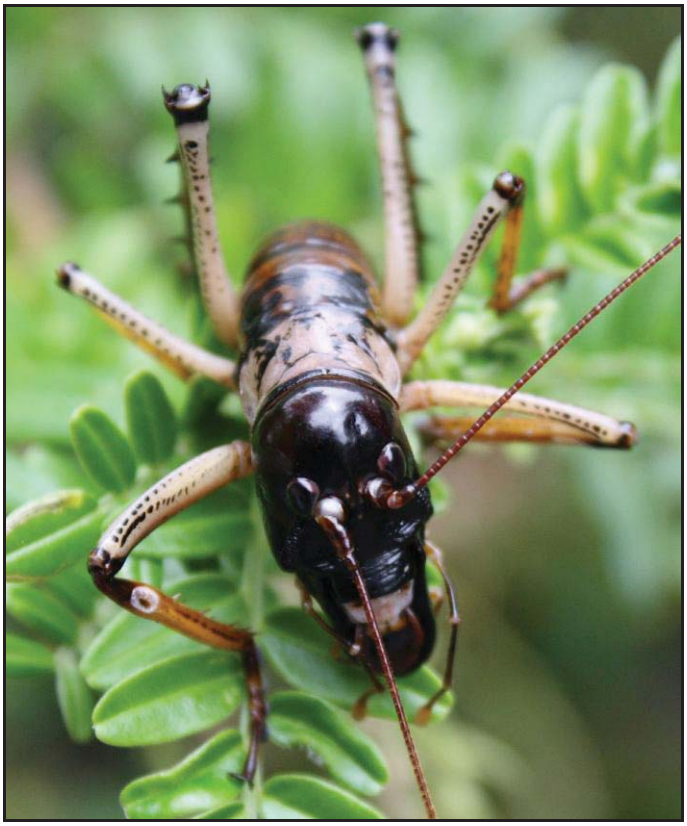
In order to test for morphological and physiological differences between *Hemideina crassidens* and *H. thoracica*, this thesis has been split into three parts, each involving a different approach:

1. **Distribution of tree weta**: A new distribution map of *H. crassidens*, *H. thoracica* and *H. trewicki* in the North Island, New Zealand is produced. Mapping of the known locations of the three species allows comparisons of environmental parameters of each species' habitat. Evidence of morphological variation within *H. crassidens* and *H. thoracica* is presented.

2. **Growth rate and size differences:** Using an experimental approach I have compared growth rates of *H. crassidens* and *H. thoracica* when raised at two constant temperatures. Comparisons are made within and between species, populations, temperatures and sexes.

3. **Comparison of metabolic activity:** Oxygen consumption of *H. crassidens* and *H. thoracica* are compared between species and populations as well as at two different controlled temperatures.

2 The distribution of three species of tree weta: *Hemideina crassidens*, *Hemideina thoracica* and *Hemideina trewicki*.



2.1 Introduction

2.1.1 Distribution

Species distributions are influenced by both biotic and abiotic factors. Environmental variables such as temperature and precipitation change with both altitude and latitude whilst altitude additionally enforces changes in atmospheric pressure, turbulence and ultra violet radiation (Hodkinson, 2005) and, of course, physical barriers also limit dispersal. Species are also constrained by biotic factors such as competitive interactions with other taxa, and the availability of appropriate food (Bale, 2002; Case, et al., 2005).

Distribution is not spatially inert and as a result ranges may expand, contract and shift in response to any individual or combination of biotic and abiotic factors. In addition to "natural" fluctuations in conditions in space and time to which species are exposed, human induced environmental change also has an influence. Intense habitat modification such as forest clearance has a direct impact on species occupation (Ingham & Samways, 1996), but the more subtle and potentially insidious influence of human-induced climatic change is increasingly recognised as relevant to species distributions (Bale, et al., 2002). With the recent interest in global warming, studies have shown that temperatures have risen globally by 0.6-0.7°C over the past 100 years (Bale, 1996; McGlone, 2001), with predictions that they may rise another 1.4°C-5.8°C by 2100 (Bale, 2002). This increase may have little effect on those species that already cover a large climatic range, as they may be 'preadapted' to change, however, species with narrow climate tolerance, such as those in cold or montane habitats, are likely to show the largest effects of increasing temperature (Bale, et al., 2002). Depending on levels of existing variation and the rate of change, global warming has the potential to result in adaptation, range shifts or local extinctions.

Global climate change during the Pleistocene (2.6 million years ago – 12,000 years before present) has followed more than 11 Milankovitch cycles which is a predictor of regular climate change due to the position of the earth, sun and other planets (Bennett, 1990). A changing climate is likely to have had a significant effect on distributions of New Zealand animal populations in the recent past. Alloway, et al. (2007) analysed climate in New

Zealand over the past 30000 years through tephrochronology. They marked six major changes in climate over this time (Figure 2.1): 1. The last glacial coldest period (28000 to 18000 years ago); 2. a late glacial warming (18000 to 13500 ya); 3. a late glacial reversal (13500 to 11600 ya); 4. an early to mid-Holocene cooling (11600 to 6500 ya); 5. a mid-Holocene cooling and variability (up to 6500 ya); and 6. a late Holocene warm event (900-500 ya).

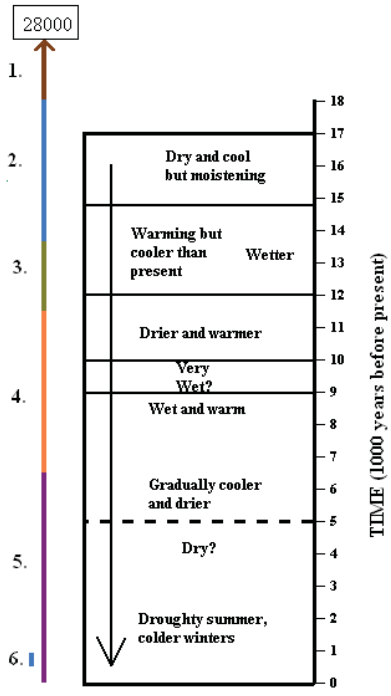


Figure 2.1 An historical overview of New Zealand's changing climate (Newnham, Lowe, & Williams, 1999)

Most notably, climate affected the vegetation throughout the North Island, expanding podocarp/broadleaf forest to cover the majority of the land area (Figure 2.2) which influences the distribution of those populations which rely on specific tree species for shelter or food. Additionally, glaciation has moulded the New Zealand landscape and encroached on vegetated areas, possibly causing pockets of populations to survive as relics, separated from the rest of the population by untraversable and unsuitable habitat. This isolation can lead to population differentiation via drift and/or selection. Depending on the length of time, level of gene flow and divergent selection, distinct species may result from climate-induced subdivision of populations.

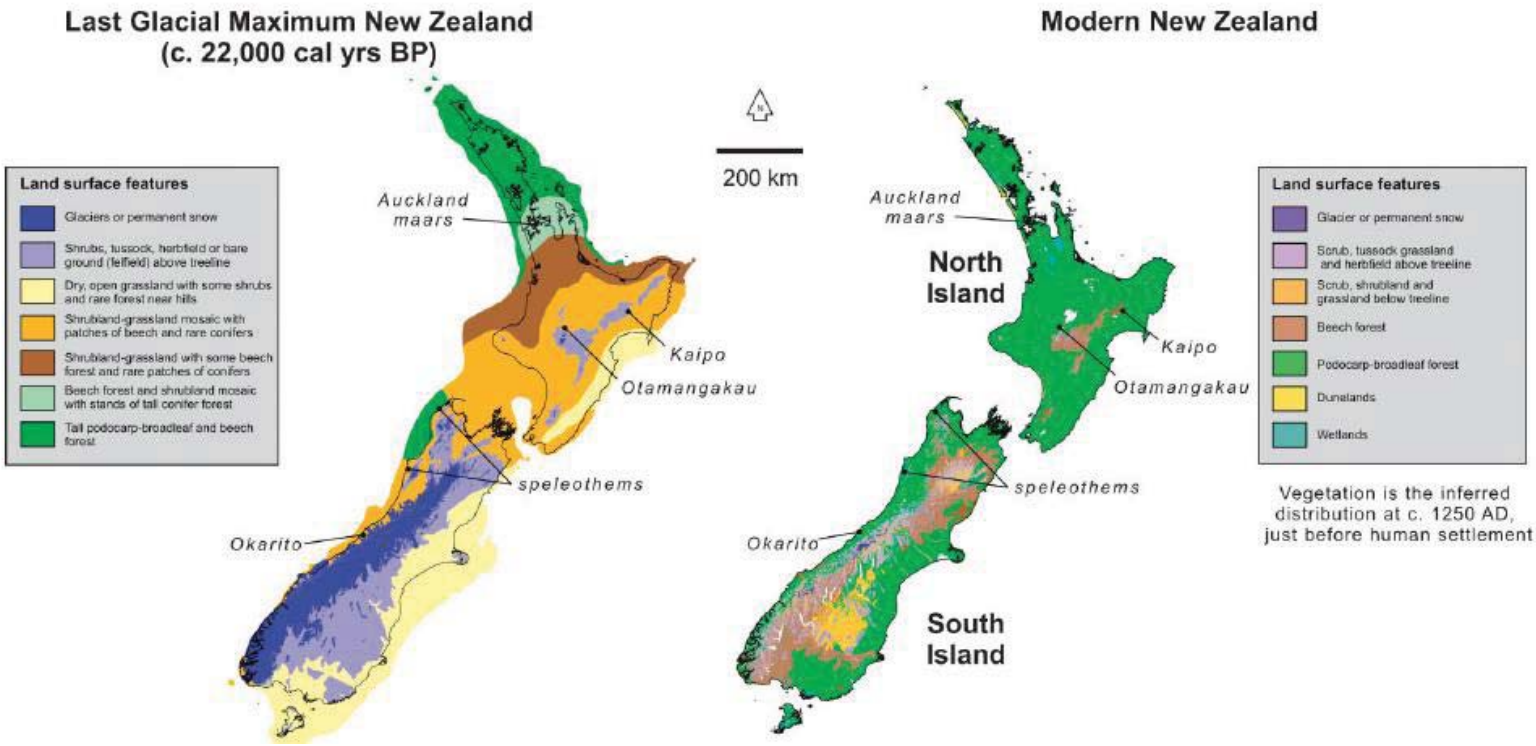


Figure 2.2 Proposed and existing high resolution vegetation zones in New Zealand (Barrell, Alloway, Shulmeister, & Newnham, 2005)

2.1.2 Size Clines

The average body size of individuals within a species may follow a trend based on latitude which is seen as larger-sized animals at more southern latitudes (in the southern hemisphere) when compared to body size in more northern latitudes. This was first described by Bergmann in 1847 who stated that races of a species are often larger in colder environments (Angilletta Jr, Steury, & Sears, 2004; Blanckenhorn & Demont, 2004). This "rule" was developed specifically with endothermic animals in mind, because increased energy efficiency results from smaller surface area to volume ratio so that larger individuals are better able to conserve heat (Blanckenhorn & Demont, 2004). Thus Bergmann's rule predicts size clines will be correlated with temperature clines. Since this theory has been well supported in literature, it was extended to include ectotherms and has been supported by laboratory studies that show increasing size with decreasing temperature due to what is probably phenotypic plasticity (Angilletta Jr, et al., 2004; Atkinson, 1994). This is in contrast to optimal size models which suggest that adult maturity will come at a smaller size in environments which impede growth (Angilletta Jr, et al., 2004). However, the rule is not universal as some studies of ectotherms show converse-Bergmannian size clines e.g. the common toad *Bufo bufo* (Cvetkovic, Tomasevic, Ficetola, Crnobrnja-Isailovic, & Miaud, 2009).

Contrary to Bergmann's theory, converse-Bergmannian clines are thought to be influenced by growing season rather than temperature and predict that animals in a cooler climate will mature at a smaller size due to the need for rapid growth during a short growing season (Blanckenhorn & Demont, 2004). Thus, this is not a plastic response to conditions but an evolutionary outcome of selection in favour of earlier-maturing individuals. This hypothesis appears to be the most supported of the two in Orthoptera (Whitman, 2008), but distinguishing the causes of size clines from distribution data alone is usually not possible.

The North Island of New Zealand supports three species of tree weta (Insecta, Orthoptera Anostostomatidae): *Hemideina crassidens*, *H. thoracica* and *H. trewicki*, which have, for the most part, parapatric distributions. *Hemideina crassidens* and *H. thoracica* do appear to

have intersecting distributions where their ranges meet, and are even known to share roost holes in that contact area (Trewick & Morgan-Richards, 1995). The Wellington tree weta, *H. crassidens*, is found in the lower North Island with outlying populations in Taihape, Dannevirke, Taranaki and Ruapehu as well as in the west of the South Island, down to Lake McKerrow and Hollyford River Valley (Trewick & Morgan-Richards, 1995). The Auckland tree weta, *Hemideina thoracica*, is distributed throughout the upper two thirds of the North Island with a southern population near Levin. *Hemideina trewicki* (Hawke's Bay tree weta) is restricted to the eastern Hawke's Bay, where several populations exist in sympatry with *H. thoracica* (Trewick & Morgan-Richards, 1995, 2000).

The distribution of the two dominant tree weta species in North Island, New Zealand, *Hemideina crassidens* and *H. thoracica,* was first mapped by Trewick and Morgan-Richards (1995) (Figure 2.3). From their respective distributions it was suggested that *H. crassidens* has been displaced via competitive exclusion from central North Island by expansion of the range of the warm-adapted species *H. thoracica*, due to climate change during the current interglacial. Evidence for this idea comes from the high altitude populations of *H. crassidens* that are surrounded by *H. thoracica* (Trewick & Morgan-Richards, 1995), and the genetic signature of range expansion seen in *H. thoracica* (Morgan-Richards, Trewick, & Wallis, 2001). In the 16 years since, additional sites have been sampled and the ecological interactions between tree weta at several of those sites have been further elucidated. By adding to the known locations of *Hemideina crassidens* and *H. thoracica* and studying the environments with which each is associated, we hope to further understand the competitive interactions and vulnerability to environmental change of these species. Here we develop distribution maps of these two species, examine ecological correlates and evidence of size variation in concordance with climatic variables and therefore hypothesize what impact global warming may have on the species' ranges. For completeness, the third species of tree weta found in the North Island, *H. trewicki*, will also be mapped, although the interactions of this species with the others are not of interest in this thesis.

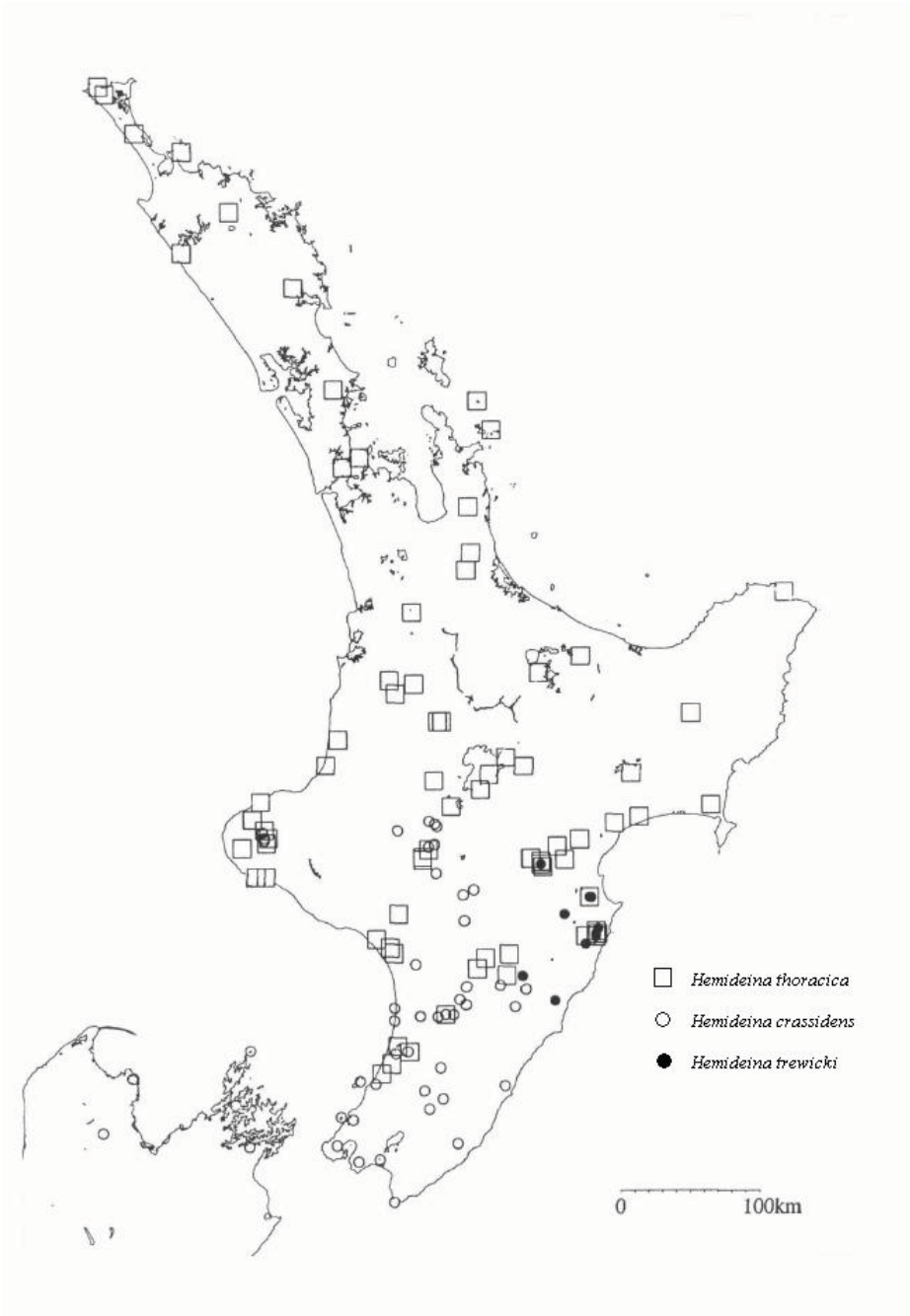


Figure 2.3 Distribution of tree weta in the North Island of New Zealand, from Trewick and Morgan-Richards (1995).

2.2 Methods

2.2.1 Weta Collections

Tree weta were collected from various sites throughout New Zealand over a period of 20 years and identified through differences between species in the colour of their pronota and abdomens. In some instances, specimens were brought back to the lab and preserved in a collection for future reference. The collection of tree weta was by hand during daylight from likely roost holes over a period of time from 1990 until the present. The data included here comes from both published (Trewick & Morgan-Richards, 1995) and unpublished (Jacobson, 2009) work as well as from recent collections by the author. On collection, species, sex, and location data were recorded and tibia length and weight were documented to assess size and therefore instar. Weight was taken as an overall indication of mass as it was convenient in field locations and tibia length has been used as a reliable size measurement due to the ease of access (weta can be measured alive c.f. testis/ova) and the lack of malleability of the limb which limits human error. Sexually mature tree weta (adults) were distinguished by morphological characteristics of sharp, curved, shaded ovipositors in females and by curved cerci in males (M. Morgan-Richards, personal communication. February 10th 2010). Any irresolute individuals were tested for sexual behaviour against known adults of the opposite sex (Spencer, 1995).

Because of the interest in interactions between *Hemideina crassidens* and *H. thoracica*, additional collections were made focusing on the distribution of the two species on Mount Taranaki which took place at the contact zone along the three transect roads and involved more intensive searching. Weta from Mount Taranaki were initially systematically searched for on roads up the mountain (Manaia and Pembrooke) by placing semi-permanent tags every 200 metres (a total of 18 tags between 600 and 893 m asl on Manaia Road and 16 tags from 650 to 862 m asl on Pembrooke Road). Each of these 200 m stretches was divided into 50 m search areas that penetrated the vegetation five metres from the road on both sides. Weta roost holes were then identified within these search areas and weta were hand collected during daylight. Furthermore, artificial weta roosts were placed at each tag site to enable easy collection of individuals inhabiting these roosts in future studies.

Additional weta from Mount Taranaki were also collected from Egmont Road and Wilkie's Pools Loop track by hand collecting.

2.2.2 Geographical Information Systems (GIS)

Distribution maps were created from data collected as described above using ArcSoft GIS version 9.3.1. Additionally, Land Environments New Zealand (LENZ) (Leathwick, et al., 2003) level one layers were used to infer the annual mean and minimum temperatures at the sampled sites. LENZ is an environmental classification system which takes multiple environmental data sources to interpolate a map of conditions present in any area. Included in these conditions are annual mean temperature and minimum annual temperature which may be mapped separately and merged with overlying layers to map associations of species with climates.

Maps of size distribution were also created using the methods above for individual adult specimens that had size information available (tibia length) and once completed, arbitrary geographic divisions were made within species to enable testing of size means between the groups based on latitude. To compare and contrast size distribution by latitude, minimum and mean annual temperature data were retrieved from the LENZ database for the location of each individual specimen previously mapped. This was graphed to show the temperature distribution of each species of tree weta.

2.3 Results

2.3.1 Distributions of three tree weta species in New Zealand

Since 1995, many more geographical areas have been sampled and thus the distributions of all three tree weta species in the North Island of New Zealand have been more thoroughly revealed. *Hemideina thoracica* is now mapped as more widely distributed from Auckland north, being located in both coastal and inland areas of the upper North Island. This species has also now been recorded around the East Cape area and on off-shore islands (Red Mercury and Cuvier). *Hemideina crassidens* is now documented as being distributed deeper into the South Island (now as far south as Haast), as well as being recorded further north in

the Whirinaki frost flats (Figure 2.4) where it is entirely surrounded by *H. thoracica*. This scenario also occurs on Mt Taranaki and Mt Ruapehu where *H. crassidens* remains isolated on the upper altitudes, completely surrounded by *H. thoracica* at lower altitudes. The range of *Hemideina trewicki* is now known to extend to Cape Kidnappers on the eastern Hawke's Bay coast. On Mt Taranaki, the contact zone between *H. crassidens* and *H. thoracica* shows a relatively abrupt contact with little overlap between the two species (insert, Figure 2.4).

The additional detail of the contact zone on Mt Taranaki has enabled monitoring of altitudinal distributions over time and indicates a change in ranges. The southern aspect (Manaia Road) has seen an upwards range shift for both species and a reduction of overlap from 40 metres at the contact zone in 1995 to only 14 metres in 2008/2009. Similarly, the eastern aspect (Pembrooke Road) shows an upward shift and where the species were separated by 30 metres of habitat between them in 1995, they now not only make contact but overlap by six metres. The northern aspect of Mt Taranaki (Egmont Road) differs in that it shows a downward shift in ranges but has also gone from ten metres of uninhabited space between species in 1995 to an overlap of three metres in 2008/2009 (Table 2.1).

Table 2.1 Relative altitude of distributions of *Hemideina thoracica* and *H. crassidens* on the three aspects of Mount Taranaki in 1995 and 2008/2009.

	ALTITUDE 1995 (m asl)	**ALTITUDE 2008/2009 (m asl)**
	H. thoracica/H. crassidens	*H. thoracica/H. crassidens*
Manaia (s)	690/650	803/789
Pembroke (e)	780/810	828/822
Egmont (n)	930/940	918/915

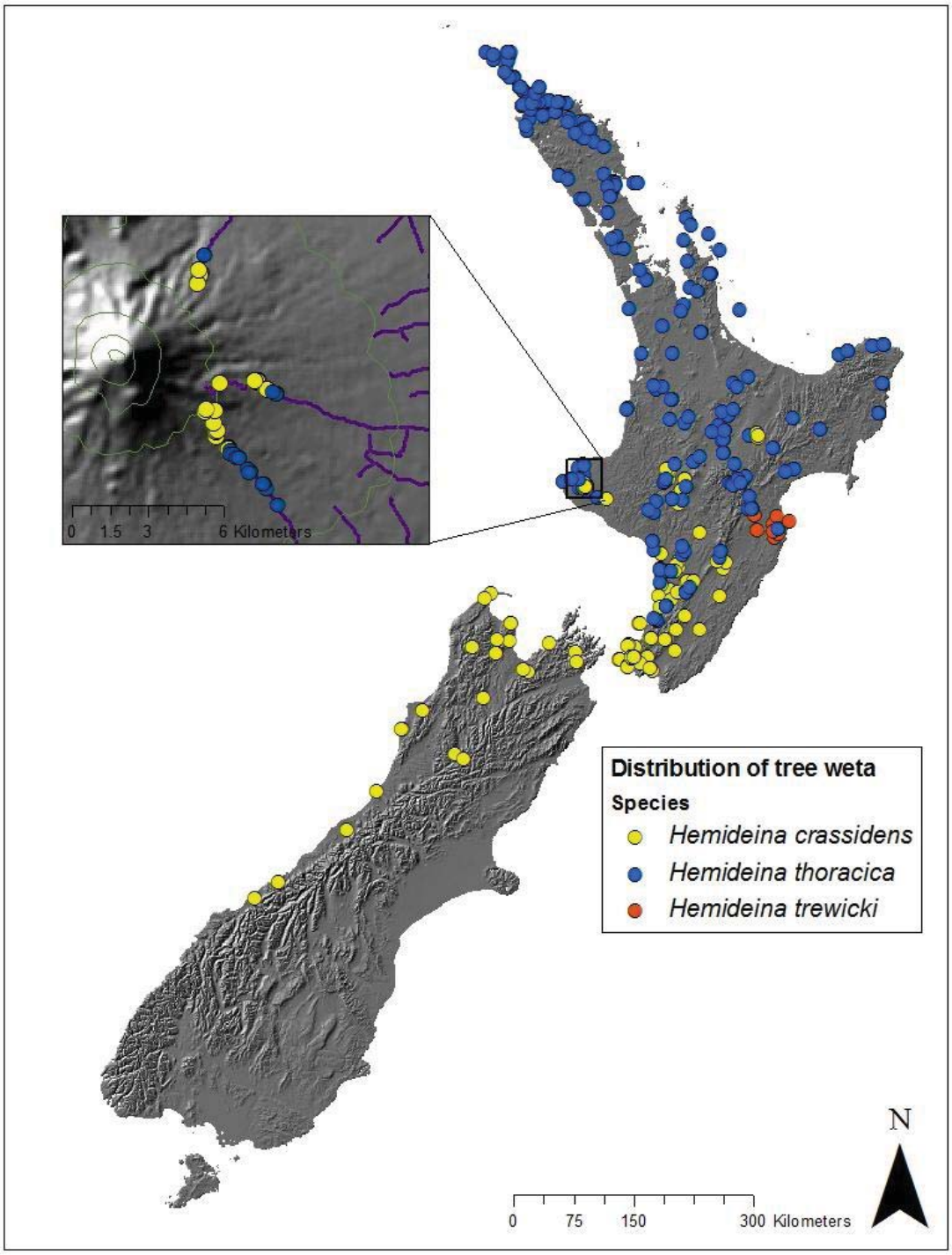


Figure 2.4 Distribution of tree weta species *Hemideina crassidens*, *H. thoracica* and *H. trewicki* in New Zealand with insert showing detail of altitudinal distributions of *H. crassidens* and *H. thoracica* at contact zone of the two species on Mount Taranaki (see table 2.1 for altitudinal distribution).

2.3.2 Latitudinal size clines in tree weta

Additional to the distribution of *Hemideina thoracica* and *H. crassidens*, we have explored Bergmann's theory of increasing size with increasing latitude. This was achieved by recording tibia lengths in adult tree weta either in the field or from preserved specimens (Figure 2.5 and Figure 2.6). As an effect, sex is unlikely to cause a difference in tibia lengths, as the dimorphic differences between male and female tree weta are observed solely in the head region.

The mean tibia length of adults does differ significantly between species, with the southern species on average longer-legged than the northern species; *H. crassidens* 21.24 mm and *H. thoracica* 20.46 mm (two sample t-test, $P = 0.022$).

A two-sample t-test of tibia lengths of *H. crassidens* specimens divided into arbitrary groups of North Island and South Island showed no significant difference in means ($P = 0.733$, DF= 17; 21.31 ± 0.30mm, 21.08 ± 0.58mm respectively) (Figure 2.7). A two-sample t-test of tibia lengths of *H. thoracica* specimens collected north and south of Auckland (latitude ≈ -40°) showed a significant difference in the mean size of individuals ($P < 0.001$, DF= 119; Figure 2.8). *Hemideina thoracica* north of Auckland had a shorter mean tibia length (mean= 19.73 ± 0.24 mm) than those found south of Auckland (mean= 22.13 ± 0.25 mm).

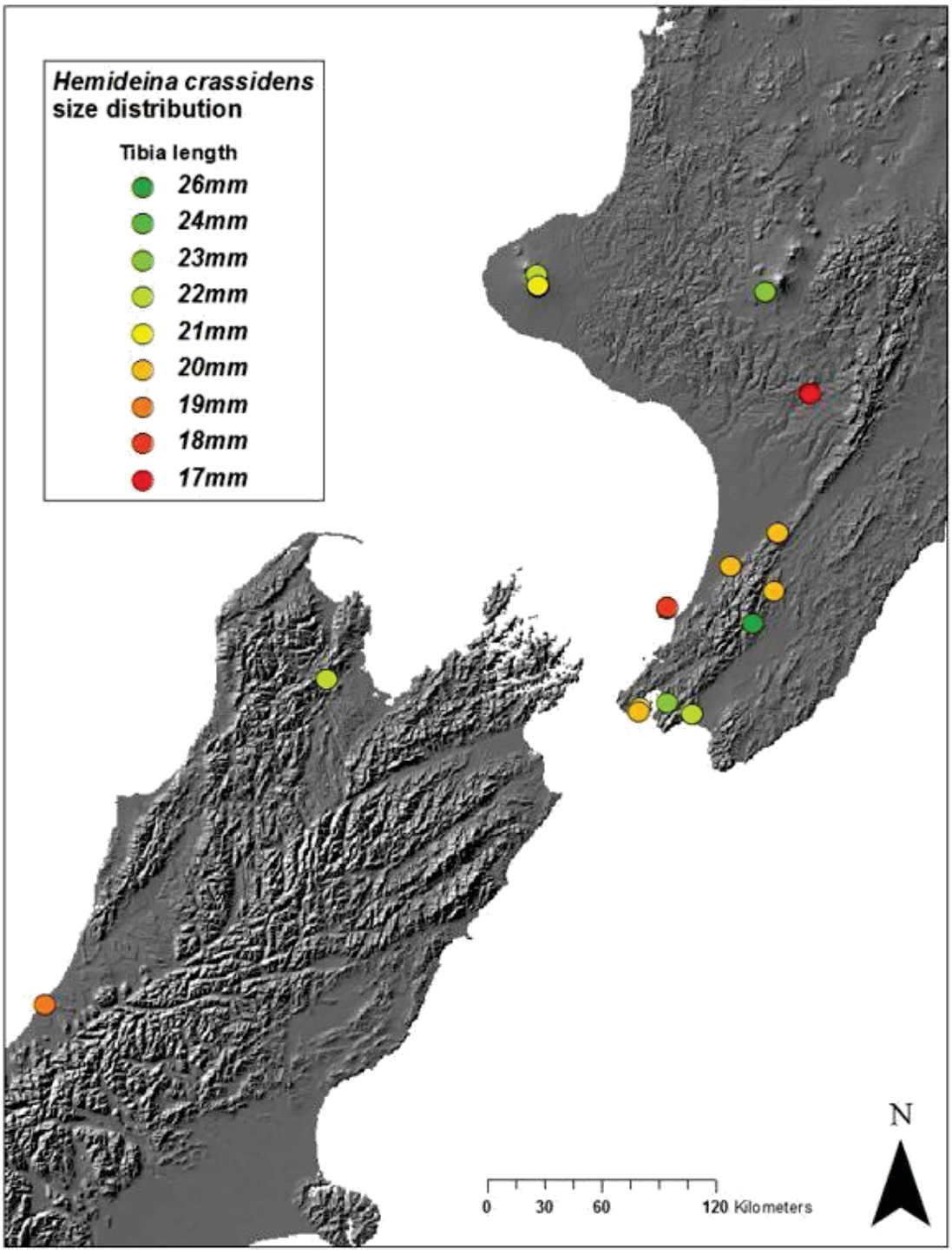


Figure 2.5 Geographical distributions in size (tibia length) of individual, adult tree weta *Hemideina crassidens.*

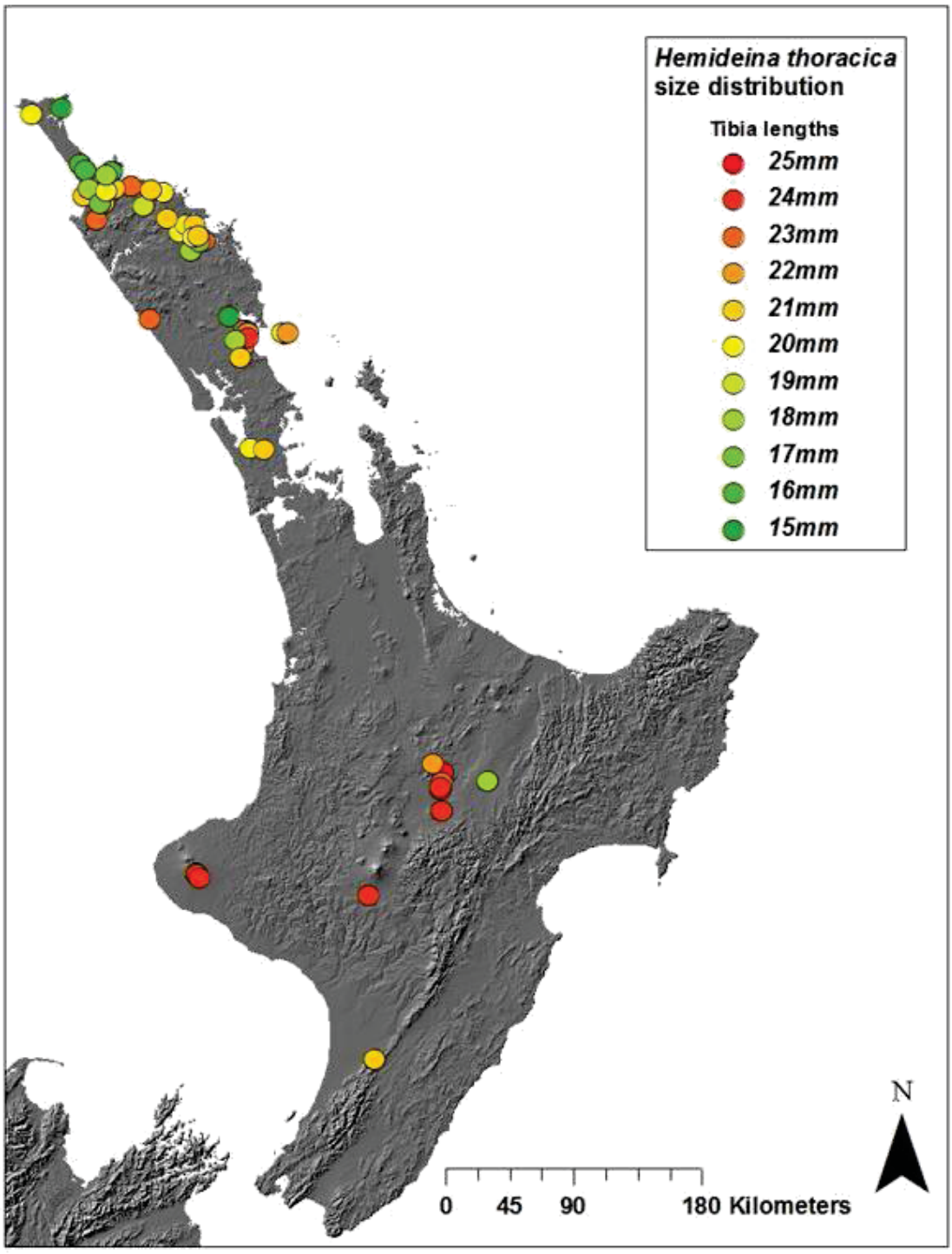


Figure 2.6 Geographical distributions in size (tibia length) of individual, adult tree weta *Hemideina thoracica*.

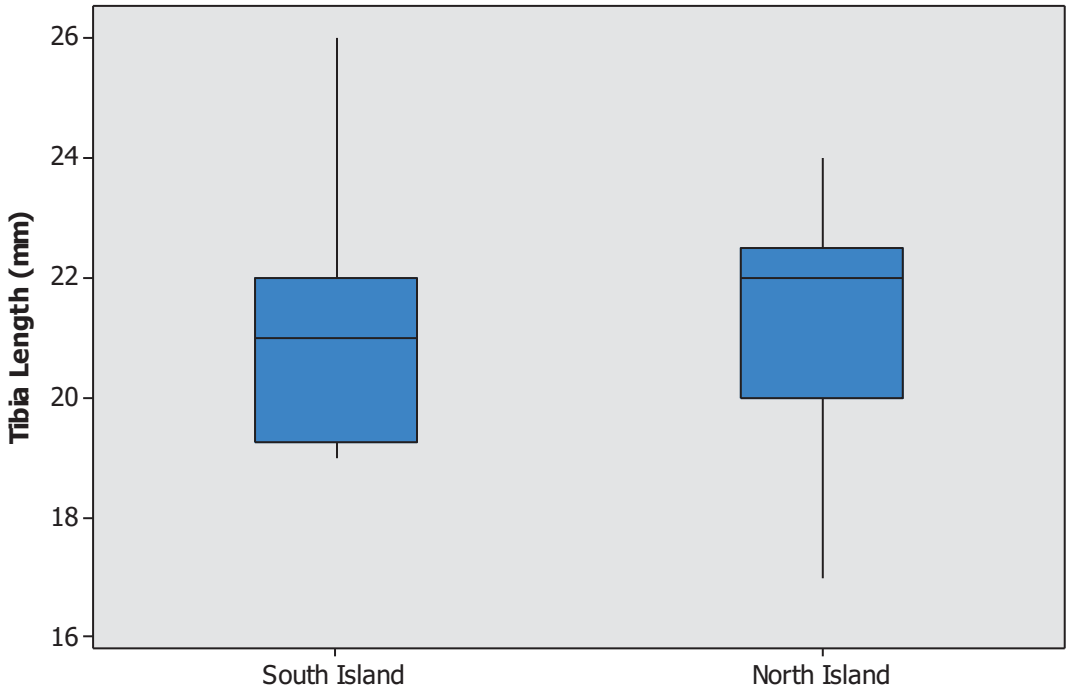


Figure 2.7 Distribution of adult *Hemideina crassidens* showing size (tibia length) variation with latitude. South Island n = 12, North Island n = 29.

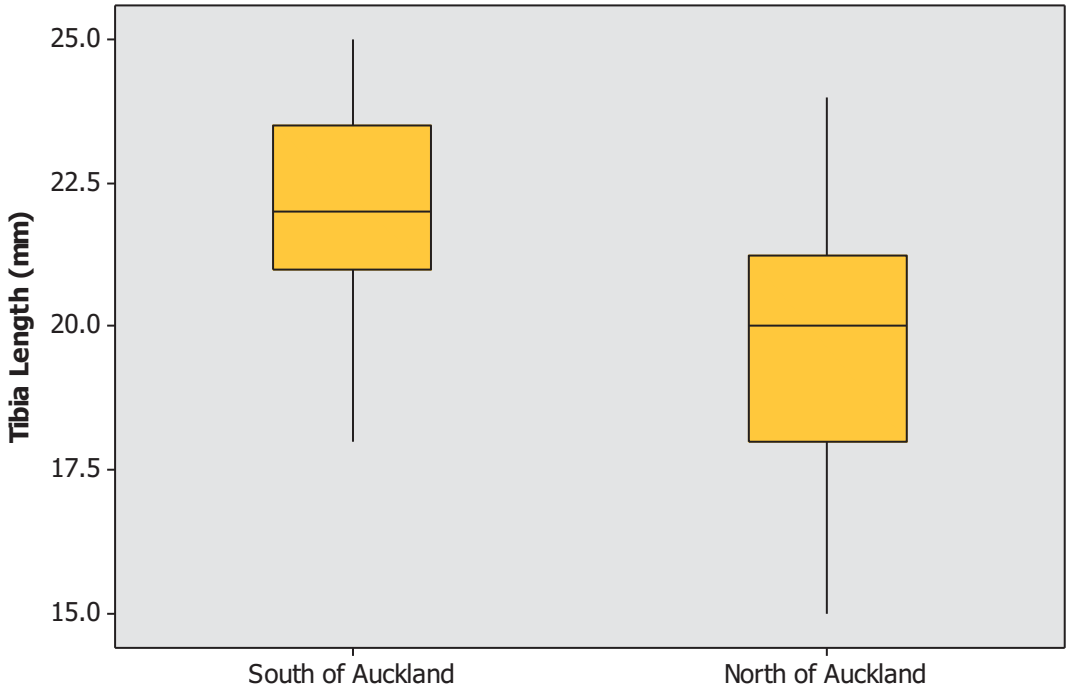


Figure 2.8 Distribution of adult *H. thoracica* showing size (tibia length) variation with latitude. South of Auckland n = 45, North of Auckland n = 102.

2.3.3 Temperature size clines in tree weta

Hemideina thoracica showed a significant negative correlation between mean annual temperature and tibia length ($y = -0.8825 x + 32.381$, $R^2 = 0.2201$, $P < 0.001$) although *H. crassidens* did not ($y = 0.3933 x + 16.677$, $R^2 = 0.0314$, $P = 0.268$; Figure 2.11). Minimum annual temperature and tibia length were significantly negatively correlated for *H. thoracica* ($y = -0.7748x + 24.056$, $R^2 = 0.2221$, $P < 0.001$) but not for *H. crassidens* ($y = 0.2782x + 20.579$, $R^2 = 0.0163$, $P=0.426$; Figure 2.12).

A one-way ANOVA with Tukey's test of mean minimum temperature between the three species shows that the total mapped distribution of *Hemideina thoracica* differs significantly from that of both *H. crassidens* (Table 2.2) and *H. trewicki* although *H. crassidens* and *H. trewicki* do not significantly differ in mean minimum temperature of their ranges. A one-way ANOVA with Tukey's test of mean annual temperature between the species shows that the total mapped population of *H. crassidens* differs significantly from *H. thoracica* but not *H. trewicki* (Table 2.2). Additionally, *H. thoracica* and *H. trewicki* do not differ significantly.

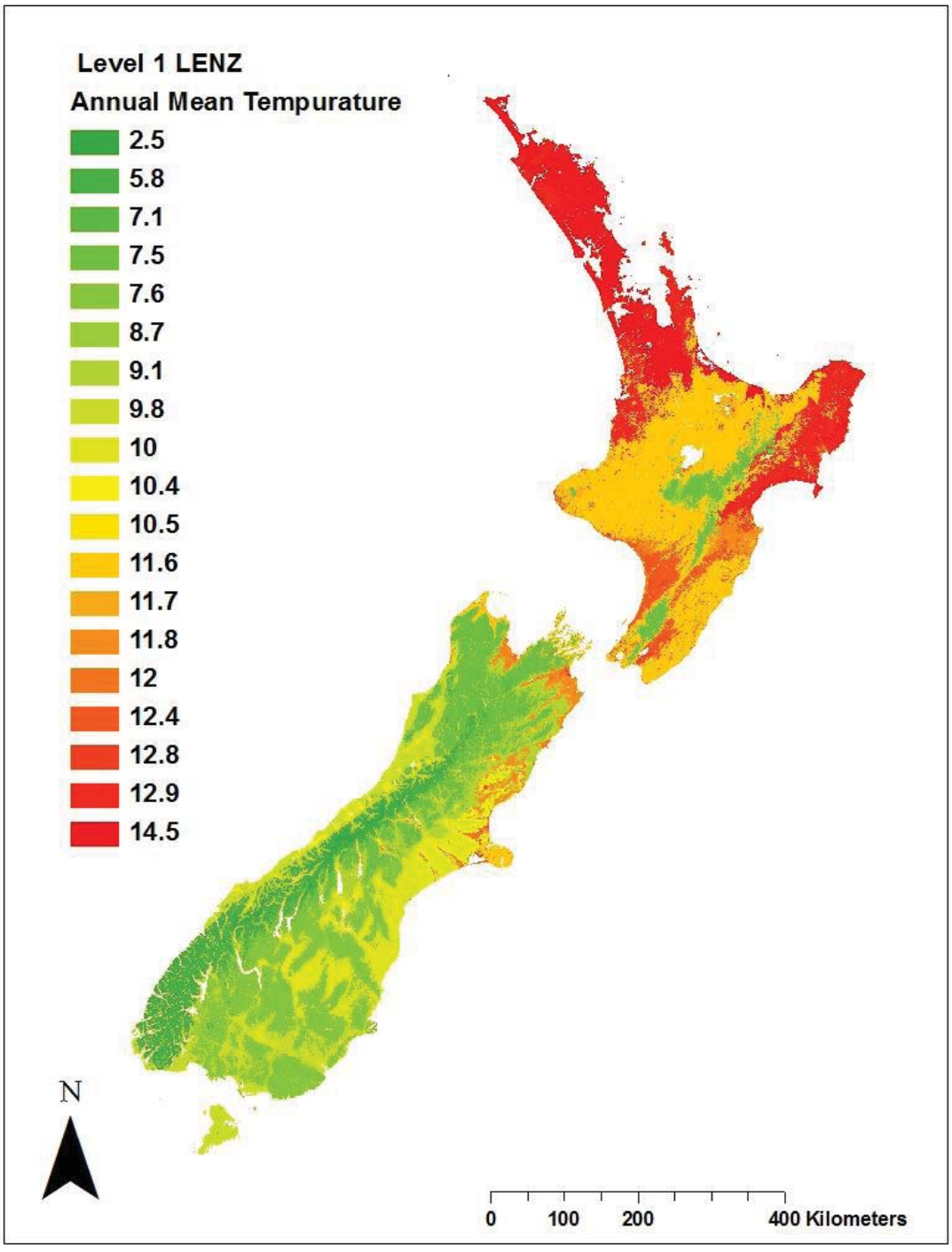


Figure 2.9 LENZ map of mean annual temperature (°C) of regions of New Zealand.

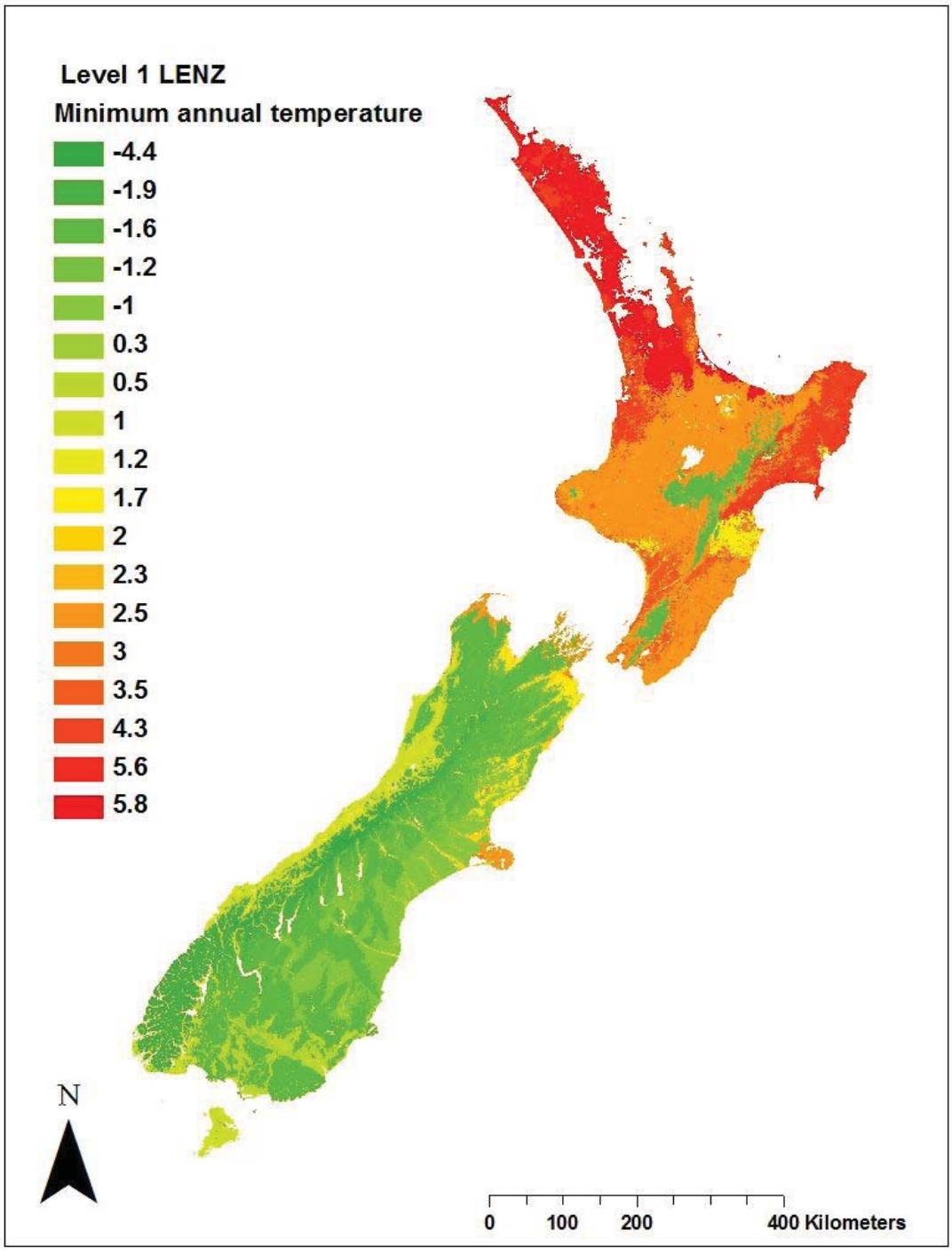


Figure 2.10 LENZ map of minimum annual temperature (°C) of regions of New Zealand.

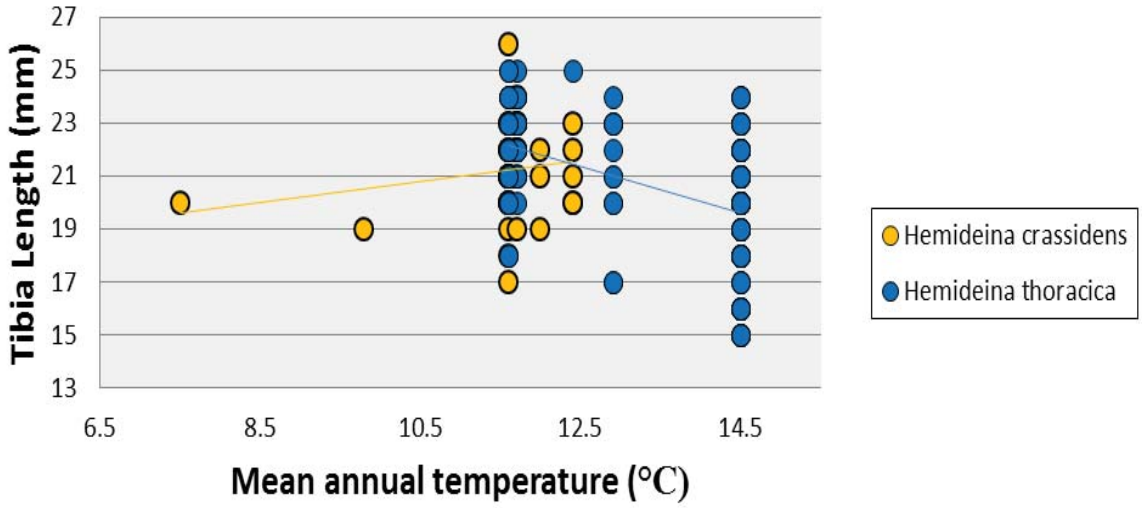


Figure 2.11 Size clines in *Hemideina crassidens* and *H. thoracica* based on a LENZ layer of mean annual temperature at the collecting site and tibia lengths of adult specimens.

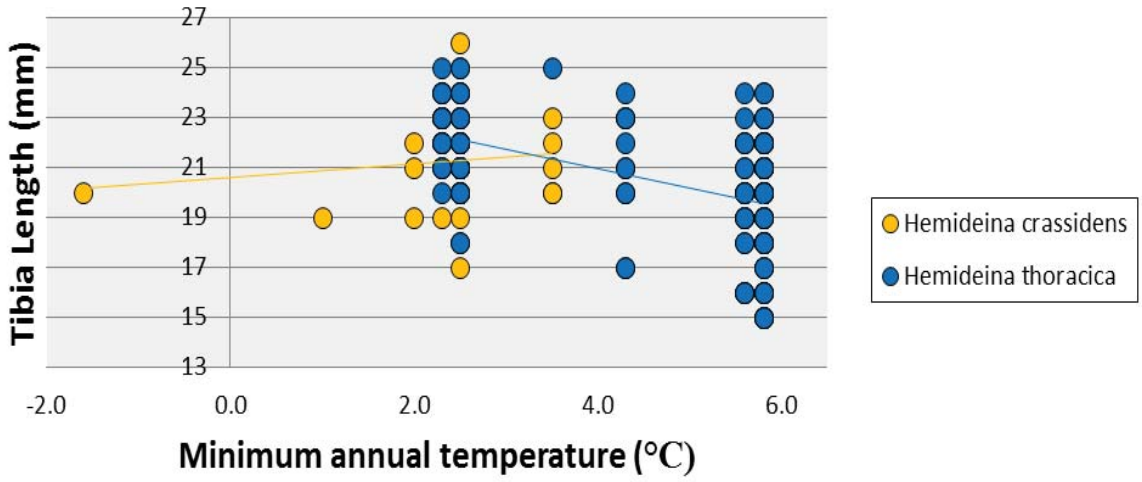


Figure 2.12 Size clines in *Hemideina crassidens* and *H. thoracica* based on a LENZ layer of minimum annual temperature at the collecting site and tibia lengths of adult specimens.

Table 2.2 Mean temperatures of sampled populations of *Hemideina crassidens*, *H. thoracica* and *H. trewicki* based on level one LENZ layers. * And # denotes a statistically significant difference between means in columns.

	Mean minimum temperature (°C) (Range)	**Mean annual temperature (°C) (Range)**
Hemideina crassidens	**2.353* ± 0.05** (-1.6-3.5)	**11.538*# ± 0.05** (7.5-12.8)
Hemideina thoracica	**3.807*# ± 0.08** (-1.6-5.8)	**12.758* ± 0.07** (7.5-14.5)
Hemideina trewicki	**2.242# ± 0.34** (1.7-5.6)	**12.192# ± 0.24** (11.8-14.5)

2.4 Discussion

The tree weta in this study were found in both artificial and natural roost holes in a variety of vegetation. Most tree weta specimens were recorded in native trees with an apparent preferance for *Pseudopanax* sp, however, tree weta have also been reported in *Pinus* plantations where they apparently subsist on the exotic foliage (S. A. Trewick, personal communication, June 20th 2009; (Minards, 1996-2007). Collection of weta was aided by pre-established artificial roosts on Mount Taranaki where *Hemideina crassidens* and *H. thoracica* were found as well as at Mohi Bush where *H. thoracica* and *H. trewicki* were collected from roosts (Trewick & Morgan-Richards, 2000) and where the two species were seen to share a single roost. All other specimens were found using hand collecting techniques by experienced field workers.

The contiguous vegetation in the North Island appears to support a continuous habitat for tree weta and all areas sampled (with the exception of the Rangipo Desert (Trewick & Morgan-Richards, 1995)) revealed tree weta of one or two species. The gaps in distribution of tree weta in the North Island (Figure 2.4) are due to lack of sampling rather than absence of tree weta.

There appears to be few areas where more than one species of tree weta can be found. At Mt Taranaki (insert, Figure 2.4), Mt Ruapehu and the frost flats at Whirinaki two species have parapatric distributions, as 'pockets' of *H. crassidens* are found surrounded by *H. thoracica*, with very little overlap between species. I infer from these parapatric pockets that competitve exclusion keeps *H. crassidens* and *H. thoracica* from sharing the uninterrupted habitat. On the mountains the environmental gradient is steep and the overlap between the two species narrow. Conversely, Waiopehu Reserve near Levin exclusively supports the most southern population of *H. thoracica* in a remnant of native bush completely surrounded by *H. crassidens*. Sympatry of *H. crassidens* and *H. thoracica* occurs in narrow regions of the Manawatu and Wairarapa at the foot of the Tararua Ranges, where it is likely that environmental gradients are shallow and thus overlap of the species is

wider. In the Hawke's Bay region *H. thoracica* is sympatric with *H. trewicki*, and as this involves a different pair of species, competitive interactions are likely to differ.

Hemideina crassidens is the only tree weta species of the seven members of the genus in New Zealand that bridges the Cook Strait, suggesting it may have taken advantage of the lower sea levels and the relatively continuous land mass of New Zealand during the last glacial cycle, or earlier (Trewick & Morgan-Richards, 2005). Generally, *H. crassidens* occupies colder areas than the other two North Island species. It alone extends down the western side of the Southern Alps and it is also located on the frost flats of Whirinaki and the higher altitudes of Mount Taranaki and Mount Ruapehu. Not suprisingly, *H. crassidens* populations occupy habitat with the lowest mean annual temperature of the three species examined (Table 2.2) although it shares a similar mean minimum temperature with *H. trewicki,* despite having a colder absolute minimum temperature. *Hemideina crassidens* may have developed adaptations to colder temperatures allowing it to inhabit colder locations from which *H. thoracica* is excluded. Despite having a closer genetic relationship with *H. trewicki* and sharing ecological characteristics with other tree-dwelling weta (Trewick & Morgan-Richards, 2005), *H. crassidens* appears to fall between the freezing tolerances of *Hemideina maori* (alpine scree weta) and *H. thoracica*. *Hemideina maori*, found soley in alpine regions of the southern South Island, has been widely studied because of its ability to withstand freezing in order to over-winter in the mountains (Ramlov, Bedford, & Leader, 1992). One study showed that in laboratory conditions, *H. maori* can survive after freezing at -9°C for 5 days, whilst *H. crassidens* endured -6.5°C for 165 minutes and *H. thoracica* tolerated -5°C for up to 150 minutes (Sinclair, Worland, & Wharton, 1999). Additionally, several *H. crassidens* individuals on Mount Taranaki have been observed in a frozen state as collections of tree weta for this study were being undertaken (pers obs).

The contact zone between *Hemideina crassidens* and *H. thoracica* on all aspects of Mt Taranaki have apparently shifted in the 16 years since it was last surveyed. Manaia and Pembrooke Roads (southern and eastern aspects) have shown an altitudinal increase in the location of contact with both species moving higher up the mountain, although on Manaia

Road *H. crassidens* has retreated more than *H. thoracica* has moved up, narrowing the contact zone from 40 metres of overlap to just 14 metres, whereas *H. thoracica* has moved a greater distance on Pembrooke Road to increase the contact between the two species to six metres. In contrast, the northern face of the mountain (Egmont Road) there has been an apparent altitudinal downward shift of both species with *H. crassidens* descending more than *H. thoracica* to allow a three metre overlap between populations. This apparent shift down the mountain may be due to limited sampling in both 1994 and 2009, as a region without weta is likely to be a sampling artifact. In contrast, on the southern and eastern transects, improved sample size would be expected to increase the area of detected overlap, rather than the observed narrowing of it. McGlone (2001) suggested that there were four ways in which climate change as an increase in mean annual temperature would affect populations in the next 100 years, of which the first, a change in latitudinal and altitudinal distributions due to the movement of populations into now habitable areas, suggests that the populations of *H. crassidens* and *H. thoracica* on Manaia and Pembrooke Roads have shifted their populations higher in response to warmer temperatures and into a more temperate climate at higher altitudes. McGlone (2001) also predicts that there will be a reduction in cold-winter habitats, even with only a moderate temperature increase, leading to a change to a subtropical climate in many lowland areas of the North Island. Presumably northern areas of the South Island will be similarly affected, although with a less-steep cold gradient, it is likely to be less severe.

Climate change is liable to impact on tree weta populations inhabiting cooler areas such as *Hemideina crassidens* found on Mt Taranaki, Mt Ruapehu and Whirinaki, which will most likely be seen as a retraction of distribution consequent to the encroaching warm-adapted *H. thoracica*. In isolated populations such as these, there is a limit to how far a cold-adapted population can retreat. On mountain peaks, the treeline restricts the habitat of herbivorous species and it is unclear as to whether or not indigenous alpine flora will gain altitude in response to climate change (McGlone, 2001). With nowhere to retreat to, cold-adapted species may be out-competed by surrounding, encroaching populations, leading to local extinctions.

This study showed no significant increase in size with decreasing latitude in *Hemideina crassidens* as hypothesised. However, *Hemideina thoracica* showed a negative correlation when tested for size against latitude which was confirmed with an observed increase in size with decreasing minimum and mean annual temperatures that follows Bergmann's rule. The lack of samples with size measurements in between the two groups (north of Auckland and south of Auckland) prevents us from differentiating between a gradient of increasing size with decreasing latitude or a decisive latitude where the size of *H. thoracica* increases.

Bergmann size clines (decreasing size with increasing temperature) are correlated in 83.5% of studies (n = 109) involving animals, plants, protists and bacteria (Atkinson, 1994). Only 11.9% of studies showed converse results, but these included the two Orthoptera species reviewed. Within the Orthoptera, converse-Bergmannian size clines appear to be more common (Blanckenhorn & Demont, 2004; Whitman, 2008); within the Gryllidae (Alexander & Bigelow, 1960; Bigelow, 1962; Bradford & Roff, 1993; Masaki, 1967; Mousseau & Roff, 1989; Ohmachi & Masaki, 1964) and Acrididae (Bidau & Martí, 2008; Telfer & Hassall, 1999) individuals get larger with increasing temperature. Theory suggests that latitudinal size clines like those seen in *Hemideina thoracica* (Figure 2.6) result from a decrease in temperature with increase in latitude. This however, is only accurate for two-dimensional geography. When the landscape takes on a third dimension i.e. altitude, temperature will vary according to height above sea level. Moreover, microhabitats will also differ from the norm, hence the need to apply fine-scale environmental information to the distribution. Altitudinally, Orthoptera appear to be more selected for smaller size with increasing altitude as seen in all species reviewed with the exception of *Melanoplus sanguinipes* (Acrididae) (Rourke, 2000), which showed a greater mass at higher altitude and *Hemideina maori* (Anostostomatidae) which showed greater head width with increasing altitude (Koning & Jamieson, 2001). Converse-Bergmannian size clines are also supported when growth is directly linked to the amount of time in the growing season, i.e. if growth takes up a considerable proportion of the growing season, then the growing season will limit growth because of constraints on resource availability (Chown & Gaston, 1999). This suggests that a short growing season will support only minimal growth, resulting in a smaller adult body size. However, this study did detect a significant size

difference between the two tree weta species with the larger species occupying the cooler distribution, and larger samples from parapatric populations might be illuminating in understanding the competitive advantage each has at different altitudes.

Hemideina thoracica are found in warmer regions of New Zealand, compared to other tree weta species. The mean annual and minimum temperature were greater where *H. thoracica* specimens were found than for either *H. crassidens* and *H. trewicki*. This may result in an increasingly southward distribution of *H. thoracica* as annual mean temperatures increase which may result in displacement of *H. crassidens* or formation of truly sympatric populations.

2.5 Conclusions

The two common tree weta in the North Island have distinct distributions with different mean temperatures. *Hemideina thoracica* is smaller in the warmer half of its range and overall this species has shorter tibia than the apparently more cold-tolerant *H. crassidens.* The distribution of tree weta in the North Island, New Zealand, is likely to change as global temperatures increase. Although large fluctuations in historical populations are inferred to have taken place, these were due to naturally cycling glacial/interglacial phases that occur approximately every 120 000 years (McGlone, 2001). This allows for the evolution of characteristics that are most parsimonious with the current climate, whereas human-induced climate change may take place too rapidly for many species to adapt, requiring a shift of populations to a more suitable habitat, or, if suitable habitat is unreachable, the demise of that population. Specifically, an increase in mean or minimum temperatures may see the distribution of *H. thoracica* shift further south as well as altitudinally higher. This may result in complete coverage of the North Island with suitable habitat for *H. thoracica* assuming that *H. crassidens* does not competitively exclude it. Without human translocation or the formation of land bridges between the North and South islands, *H. thoracica* is likely to be constrained to the North Island only.

3 A Comparison of Growth Rate among Tree Weta from Different Altitudes, Raised at Constant Temperatures.

3.1 Introduction

To maximise their fitness, individuals must reach sexual maturity and reproduce. This development is achieved in two ways: cell differentiation and cell growth (Van der Have & De Jong, 1996). Growth can only occur when there is sufficient energy to fuel cellular growth and for that, there must be a nutrient surplus after homeostatic processes have taken place. As such, insect adult body size is the outcome of three variables: egg size (determined by the preceding generation), growth rate and development rate (Van der Have & De Jong, 1996; Whitman, 2008). Each of these may be due to both genetic or environmental influences and interaction.

Geographically widespread species are able to endure a wide range of environmental conditions either through phenotypic plasticity or through genetic differences brought about by natural selection (Berner, Korner, & Blanckenhorn, 2004). In general, about 30-40% of adult body size of insects is thought to be heritable and the rest due to phenotypic plasticity (Whitman & Ananthakrishnan, 2009). Phenotypic plasticity, or acclimation when referring to physiological processes (Kingsolver & Huey, 1998), means that an animal can process real time exogenous (i.e. environmental) information and adjust its resource allocation where appropriate (Atkinson, 1994) to increase its fitness in changing climates (Kingsolver & Huey, 1998). Ultimately, natural selection will favour individuals within a population whose genetic makeup provides the most efficient growth rhythm throughout the entire growth stage (Bigelow, 1962). This may mean a fast growth rate over a relatively short growing season resulting in a smaller final size; or perhaps a slower growth rate over a longer season (in less favourable conditions) or a more rapid gain in mass to result in a larger adult body size (Fielding & Defoliart, 2007). Rapid growth can increase fitness through a reduction in generation time which reduces the chances of mortality before reproduction (Fielding & Defoliart, 2007). Optimum growth rate is achieved when there is a balance between the benefits of reaching sexual maturity and the costs of growth (Atkinson, 1994).

The rate at which an insect grows is determined by both biotic and abiotic factors such as resource abundance/nutrition (Atkinson, 1994; Fielding & Defoliart, 2007), competition (Whitman, 2008), photoperiod, water balance and temperature (Atkinson, 1994; Van der Have & De Jong, 1996; vanVoorhies, 1996; Walters & Hassall, 2006). Populations found in montane habitats are most likely to be affected by the environmental gradient which shows a decrease in temperature with an increase in altitude (approximately 6.5 degrees per 1000 metres) as well as increasing precipitation and solar radiation (Dillon, Frazier, & Dudley, 2006; Hodkinson, 2005). For an herbivorous species, these environmental gradients influence not only the insect itself, but also the host plants. When growth is directly linked to the amount of time in the growing season i.e. growth takes up a considerable proportion of the growing season, then the growing season will limit growth because of constraints on resource availability (Chown & Gaston, 1999). Primarily this will place selection on three key traits: developmental rate, growth rate and adult size (Fielding & Defoliart, 2007). This supports converse-Bergmannian size clines as it suggests that a short growing season will support only minimal growth, resulting in a smaller adult body size.

3.1.1 Physiological mechanisms of growth

Insects are contained within a rigid exoskeleton and therefore must grow allometrically through successive moultings either in a larval stage (holometabolous species) or as nymphs (hemimetabolous species). Prothoracicotrophic hormone (PTTH) and ecdysteroids in the presence of juvenile hormone (JH) control these growth processes which are stimulated by mass or food intake (Borror, Triplehorn, & Johnson, 1989; Chown & Gaston, 2010). At the beginning of the instar, JH inhibits secretion of PTTH and ecdysone, which prevents moulting. Eventually, exogenous stimuli cause the corpora allata to cease secretion of JH and levels of juvenile hormone esterase rise, causing falling concentrations of JH and the disinhibition of PTTH and ecdysone (Chown & Gaston, 2010). PTTH, which is secreted in response to photoperiod, activates prothoracic glands that release ecdysone into haemolymph, which stimulates the separation of the old cuticle from the epidermis (apolysis). The new cuticle is produced and moulting fluid begins to digest the old cuticle. Ecdysis is then triggered by a moulting hormone which causes the old cuticle to split along

fracture lines and the insect is able to step out of the old cuticle and take in quantities of air or water to expand the new (soft) cuticles until it can become sclerotized (Borror, et al., 1989). Hemimetabolous species are expected to increase appendage measurements by 1.3 times each moult (Whitman, 2008) with later instars expected to be longer than earlier instars. Given that moulting is triggered by a combination of hormones regulated by both individual size and photoperiod it is possible for weta in different environments to mature at different sizes or/and at different rates.

Due to a shorter growing season at high altitude I hypothesize that *H. crassidens* and *H. thoracica* from Mount Taranaki will show a faster growth rate compared to those from low land populations to ensure a similar final body size to lowland populations. Alternatively, tree weta from high altitude populations will demonstrate a similar growth rate than those from lowland populations but at the expense of size i.e. Mt Taranaki tree weta will be smaller at sexual maturity than those from Palmerston North. Given that I found a significant difference in adult leg length between the two tree weta species (2.3.2, this thesis) I expected *H. crassidens* to have a more rapid rate of growth rate than *H. thoracica*. This was tested for by controlling environmental conditions by raising individuals at constant temperatures in captivity. However, *H. crassidens* is found at a higher altitude on Mt Taranaki than *H. thoracica* and this might result from an advantage in growth rate of individual weta within these two populations.

3.2 Methods

3.2.1 Study animals

The animals used in these experiments were New Zealand tree weta (Orthoptera: Anostostomatidae) consisting of *H. thoracica* (Auckland tree weta) and *H. crassidens* (Wellington tree weta) collected from lowland and high altitude locations. To represent lowland individuals, both species of weta were collected over the summer of 2009-2010 from the Kahuterawa Valley, Manawatu, New Zealand (150 m asl) by hand collecting during daylight. Additional *H. thoracica* were collected by the same method from the Waiopehu Reserve, Horowhenua (150 m asl). Mount Taranaki weta were collected from

altitudes of 300-1000 m asl on Manaia, Egmont and Pembroke Roads and Wilkie's Pools Loop track between March and November 2010 by hand collecting and collecting from previously positioned artificial roosts. All weta were immature when collected, ranging from third instar to ninth instar.

Animals were kept individually in 2L containers with wire mesh fitted into the lids to allow ventilation and furnished with lengths of hollowed flax (*Phormium* species) poles as roost holes. All weta were initially kept at a 12:12 light dark cycle that was gradually extended to a 14:10 light dark cycle with the approach of summer. The weta were allowed ad libitum access to foliage of *Coprosma* sp, *Melicytus ramiflorus* (Mahoe, whiteywood) and *Prumnopitys ferruginea* (Miro, brown pine); the seasonal fruits of the afore mentioned plants and carrot. Each weta box also contained a damp square of paper towelling to provide moisture. The weta diets were supplemented weekly with soya protein (Thompson's Red 8 Protein Plus 80% nuggets).

3.2.2 Treatments

A total of 160 immature tree weta were divided into four groups: *Hemideina crassidens* from high altitude (Mount Taranaki) or low altitude and *H. thoracica* high altitude or low altitude. Each group was further divided to provide individuals raised at both 14°C and 9°C, giving a total of eight treatment groups (Figure 3.1).

Measurements of weight were recorded to the nearest mg on a Mettler AE200 scale, and left and right hind-tibia length was taken to the nearest 0.01 mm using digital Dick Smith Electronics, electronic callipers (Q1382) weekly, to sample both total growth (weight) and allometric growth (tibia length). Individuals were measured until they reached their final, adult instar. This was determined by morphological characteristics of a long, sharp, curved, shaded ovipositor in females and by long, curved cerci in males (M. Morgan-Richards, personal communication. February 10th 2010). Additionally, adult leg measurements were derived from Spencer (1995) and any irresolute individuals were tested for sexual behaviour against known adults of the opposite sex (Spencer, 1995). Once weta had

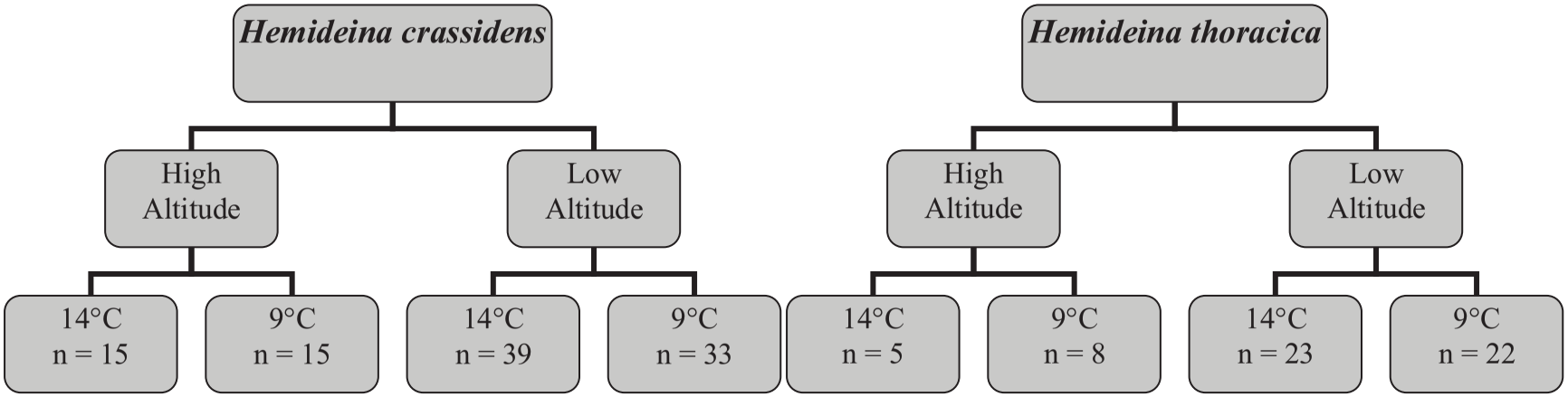


Figure 3.1 Treatment groups of *Hemideina* species weta for growth rate experiments. High altitude = tree weta from Mt Taranaki, Low altitude = tree weta from Palmerston North.

reached maturity, weight measurements were taken for an additional two weeks to allow weight to equilibrate after moulting. Male tree weta may become sexually mature at their 9th instar and will be referred to as 'early maturing males' as opposed to 'males' that have become sexually mature at the 10th instar.

3.2.3 Statistical analyses

The mean tibia lengths and body weights were calculated by averaging the length or weight of an individual tree weta over a given instar. One-way ANOVA was used to compare the tibia lengths and weights of the different treatment groups. Initial tests showed a large significant difference between the Palmerston North and Mt Taranaki groups so the data set was divided and each population tested separately.

The growth rate of each individual weta was determined by taking the mean tibia length of each instar (to correct for measurement error) or all measurement data points for mass and performing a regression against time (in weeks), giving an equation. From this, the slope is the rate of growth in either millimetres per week (tibial growth) or grams per week (total growth i.e. mass). In order to assure that the assumptions for the statistical tests were met (see below), the growth rate at each instar was compared with all other instars to test for linearity. This confirmed no significant differences between growth rates at different instars.

ANOVA analysis of this study used an incomplete factorial experimental design due to a lack of observations for some treatment combinations. Once fully modelled, a reduced model was tested with only those interactions significant to 10% in the full model being tested. The effect of sex on growth rate was tested separately by testing a model that omitted this variable and comparing the result with the full model.

Finally, the results were further analysed to test for higher (3-way) interaction terms.

Two assumptions were made in order to perform these tests:

1. The growth rate of tree weta is linear and therefore equivalently well-established regardless of the number of instars used to estimate growth rate (tenth instar growth may not be linear and was therefore only recorded for two weeks post moult).
2. Each mean in the included cross-classification table is an accurate reflection of the average response for that treatment combination, despite the different number of replicates for each combination.

3.3 Results

3.3.1 Maturation of Tree Weta

Of the 65 tree weta that reached maturity during this study, 15 were males that matured at the ninth instar (54% of males), 13 were males that matured at the tenth instar (46% of males) and 37 were females that all matured in their tenth instar. Of those early maturing males, 11 were *Hemideina crassidens* (73%- two from Mt Taranaki and nine from Palmerston North) and four (27%- all from Palmerston North) were *H. thoracica*. In a chi-squared table, these proportions of early maturing males from each population are in keeping with the sample size of the populations ($\chi^2 = 2.22$, 1 Df, $0.5 < P < 0.10$).

3.3.2 Size of weta at each instar

Initially, a one-way ANOVA showed significant differences between the Palmerston North and Mt Taranaki populations (tibia length at instar 10, $P < 0.001$; instar 9, $P = 0.017$) indicating that each population should be tested separately for size. Additionally, *Hemideina crassidens* and *H. thoracica* showed significant differences in tibia lengths (instar ten and nine $P < 0.10$) indicating that these two species should also be tested separately. This separates the data into four groups: Palmerston North *Hemideina crassidens* (HcPn), Palmerston North *H. thoracica* (HtPn), Mt Taranaki *H. crassidens* (HcTs) and Mt Taranaki *H. thoracica* (HtTs). Furthermore, each of the four groups was tested for differences between the three sexes. With the exception of HcTs instar 8, all other instars at each other group showed no significant differences between males, early maturing males and females ($P > 0.010$). The sexes at instar eight from HcTs did differ significantly

($P < 0.001$) however, with correction for multiple tests (Bonferroni correction) this was no longer significant ($P > 0.0006$). Therefore, sexes were pooled for each group.

Instar 10 shows significant differences between the species and location ($P < 0.001$) with two size groups forming (Figure 3.2). Mt Taranaki *H. thoracica* (HtTs) were larger compared with Palmerston North weta (HtPn and HcPn); however, HcTs spanned both groups. Instar nine showed no significant differences between species and locations ($P = 0.074$) with means between 18.42 and 19.36 mm. Similarly, Instar eight showed no significant differences between means ($P = 0.072$) with mean tibia lengths between 16.171 and 17.406mm.

Instar seven showed significant differences in tibia lengths ($P = 0.004$) and means fell into two groups of means. The larger group was Mt Taranaki *H. thoracica* (HtTs) compared to the smaller group containing *H. crassidens* (HcPn and HcTs). The mean tibia length of HtPn spanned both size groups. Instar six tibia lengths showed significant differences in tibia lengths ($P = 0.020$). These fell into two groups with Mt Taranaki *H. thoracica* (HtTs) being the largest, Mt Taranaki *H. crassidens* (HcTs) being the smallest and HtPn and HcPn spanning both groups. Instars five and four showed no significant differences between groups ($P = 0.361$ and 0.182 respectively) although instar five contained only three groups and instar four contained only two groups.

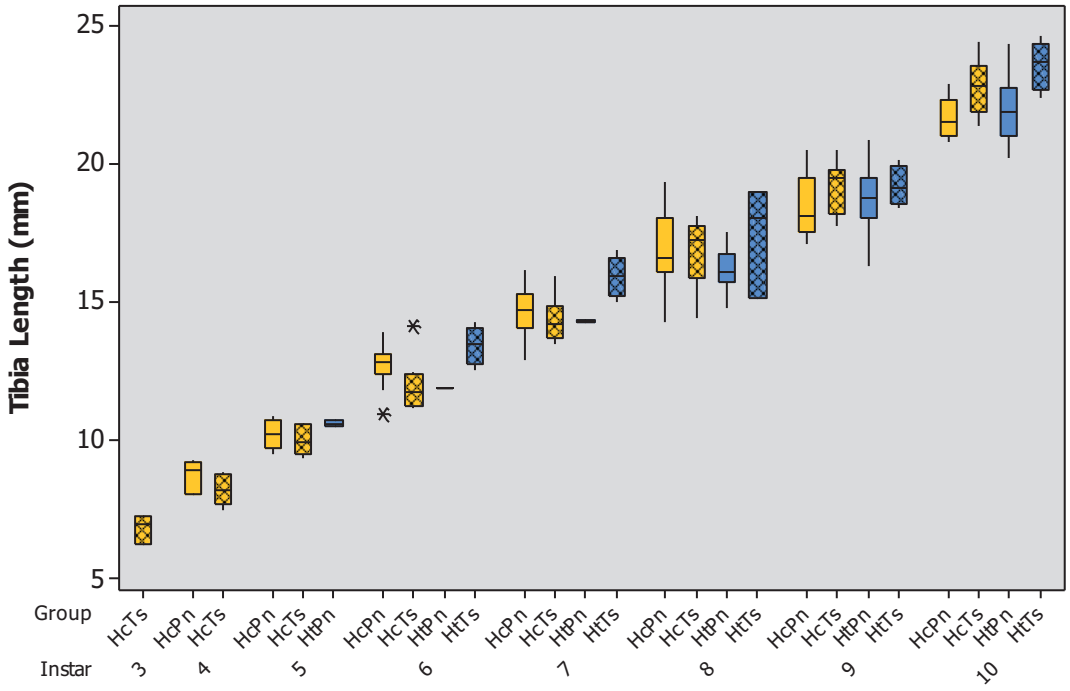


Figure 3.2 Tibia length distributions for each group at instars 3-10. X-axis abbreviations; Hc: *Hemideina crassidens*, Ht: *Hemideina thoracica*, Pn: Palmerston North (lowland) population, Ts: Mount Taranaki (high altitude) population.

As with the tibia length comparisons, there is a large weight disparity in instars ten, nine and eight ($P \leq 0.001$) with weta from Mt Taranaki showing a greater weight than those from Palmerston North. Like the tests of tibia lengths, tests for weight comparisons are separated into populations. Additionally, *Hemideina crassidens* and *H. thoracica* showed significant differences in weights (instar nine, eight and seven $P \leq 0.001$) indicating that these two species should also be tested separately. Once again, this separates the total data set into the four groups as described above. Furthermore, each of the four groups was tested for differences between the three sex categories. With the exception of HcTs instar 8, all other instars at each other group showed no significant differences between males, early maturing males and females ($P > 0.010$) and the sexes in instar eight from HcTs did not differ significantly after a Bonferroni correction. Therefore, sexes were pooled for each group.

Instars ten and nine showed significant differences between groups in weight ($P < 0.001$ and $P < 0.001$) (Figure 3.3). At both instars, the largest grouping contained HcTs and HtTs and the smallest grouping contained HcPn and HtPn. An intermediate group was also formed with HtTs spanning this and the larger group and HcPn spanning this and the smaller group.

Instar eight also showed significant differences between groups ($P < 0.001$). Two size groups formed with HcTs in the larger size group and HtPn in the smaller group. HcPn and HtTs fell into both groups. Instars seven and six showed no significant differences between mean weights ($P = 0.368$ and 0.190 respectively). Instar five was comprised of only three groups with HtTs lacking individuals at instar five. This instar also showed no significant differences ($P = 0.804$). Instar four contained only groups HcTs and HcPn but still did not show significant differences ($P = 0.550$).

Overall, *Hemideina crassidens* were heavier than *Hemideina thoracica* but with slightly shorter legs, but both species from Taranaki were larger than conspecifics from Palmerston North.

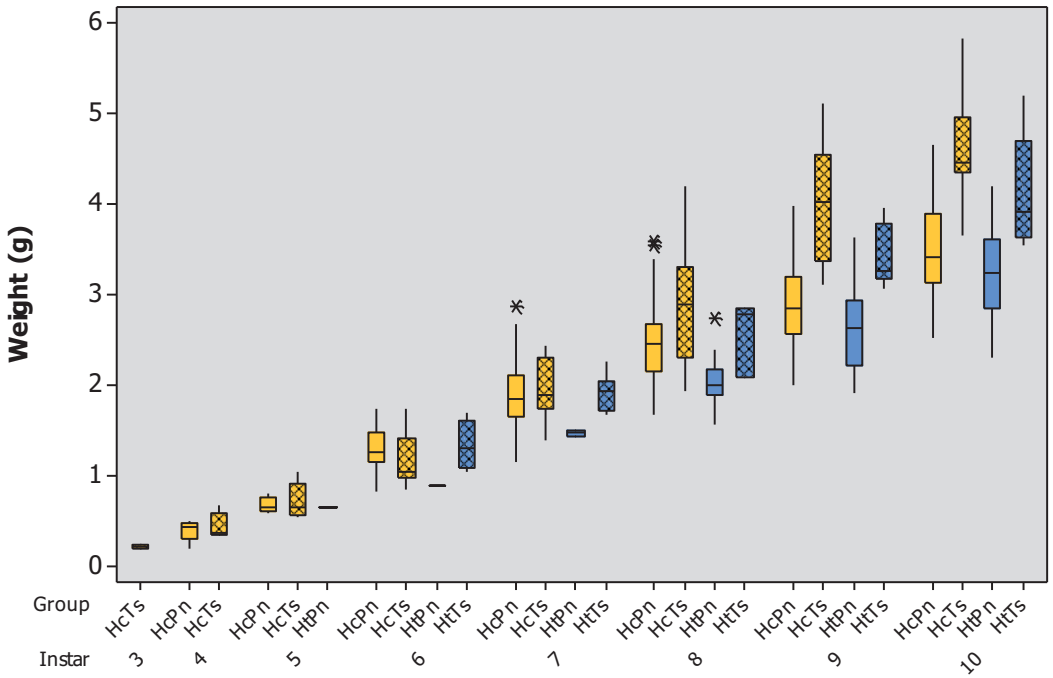


Figure 3.3 Weight distributions for each group at instars 3-10. X-axis abbreviations; Hc: *Hemideina crassidens*, Ht: *Hemideina thoracica*, Pn: Palmerston North (lowland) population, Ts: Mount Taranaki (high altitude) population.

3.3.3 Growth of tree weta under controlled conditions

Both analyses of growth rate showed that the two measurements of size produced identical results, therefore, aside from means of tibia length (Table 3.1) and mass growth rates, the results will only be shown for allometric growth (tibia length).

Table 3.1 Mean tibia growth rates (mm/week) of weta treatment groups. Pn: Palmerston North, Ts: Mt Taranaki, 14: 14°C and 6: 6°C, EM: early maturing male, M: male, F: female, Hc: *Hemideina crassidens*, Ht: *Hemideina thoracica*.

	Pn 14	Ts 14	Pn 9	Ts 9
EM Hc	0.0544	NA	0.0276	NA
EM Ht	0.01	NA	NA	0.039
F Hc	0.0227	0.079	0.0241	NA
F Ht	0.0469	0.063	0.0385	0.076
M Hc	0.0252	0.109	0.0153	0.021
M Ht	0.0034	0.071	0.0056	0.048

Of the treatments weta were subjected to during this study, temperature and collection location were shown to have a very significant effect on growth rate ($P < 0.012$) with weta from Mt Taranaki showing a significantly higher rate of growth than those from Palmerston North, when raised in identical conditions. Unsurprisingly, tree weta collected from either location showed a faster growth rate at 14°C than at 9°C. Sex was shown to be moderately significant ($P < 0.1$). However, when sex alone was tested for importance as a predictor of growth rate (see methods) it was found to not be significant ($P = 0.3239$).

The reduced model (Table 3.2) shows that the four possible variables fall into two significant pairings: temperature/population ($P = 0.009$) and sex/species ($P = 0.050$). These pairing are independent of the other pair but exclusive within the pairings. An interaction plot of temperature/location (figure 3.4) indicates that the tree weta from Mt Taranaki (regardless of species) show a higher growth rate at both 9°C and 14°C than tree weta from Palmerston North. Mt Taranaki weta also show a mean growth rate at 14°C that is over double that at 9°C whilst Palmerston North weta increase their growth rate only slightly at 14°C when compared to 9°C. The interaction plot of sex/species shows a higher growth rate of female *Hemideina thoracica* than any other group (figure 3.5). In contrast, early maturing males from the same species show the lowest rate of growth of all groups.

Table 3.2 The reduced factorial model for growth rate (tibia) of tree weta.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Temperature	1	0.012215	0.012215	6.603	0.01
Location	1	0.04617	0.04617	24.957	1.60×10^{6}
Sex	2	0.0098	0.0049	2.6486	0.07
Species	1	0.00008	0.00008	0.0433	0.83
Temp:Location	1	0.013138	0.013138	7.1019	0.01
Sex:species	2	0.011277	0.005638	3.0477	0.05
Residuals	151	0.279347	0.00185		

To test for the significance of higher interactions, residual sum of squares (RSS) values were calculated for both the full factorial model (0.26633, 141 Df) and for the reduced model (0.27846). The difference between these values (0.0121) represents the extra

variability associated with all interactions within the model, which proves to be insignificant (P = 0.625) therefore, higher interactions are not detected in this study.

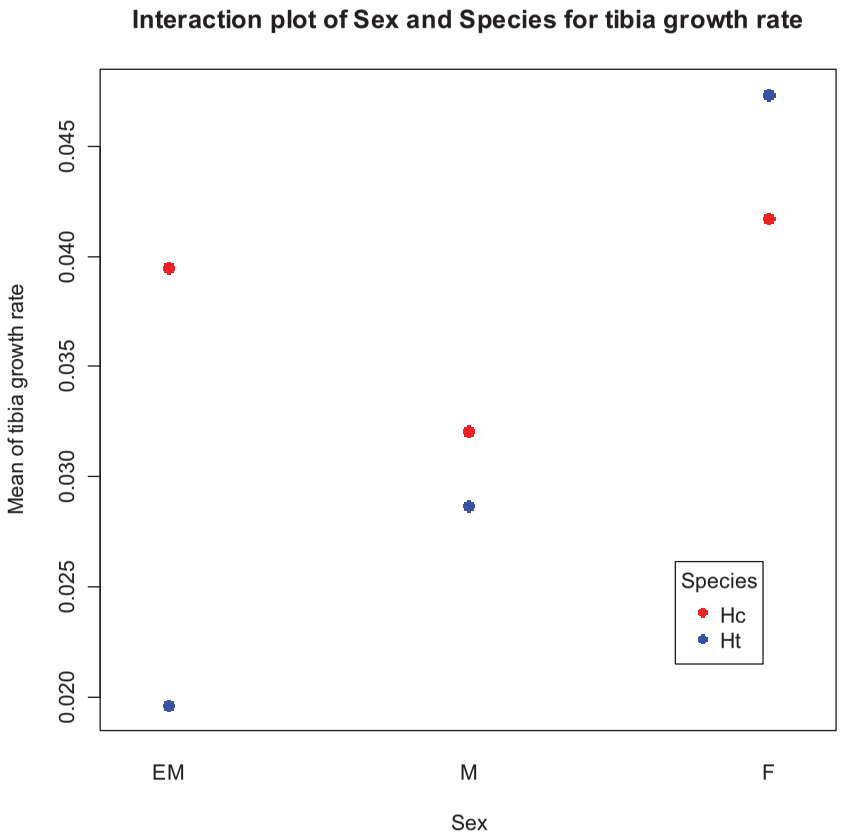


Figure 3.5 Interaction plot for tibial growth (mm/week) showing dependence of sex and species.

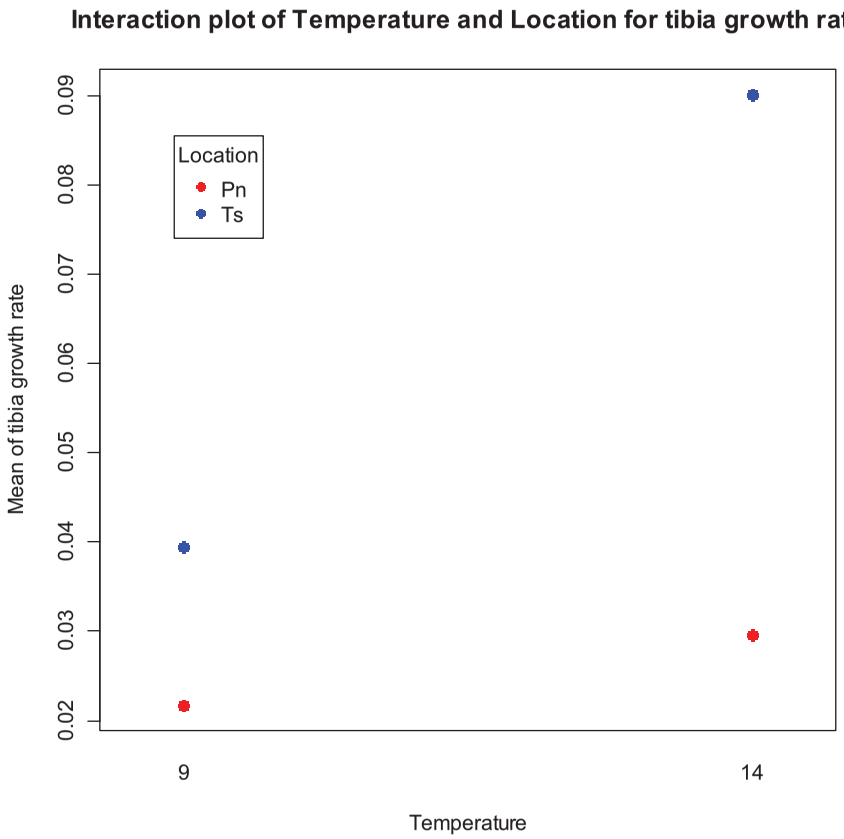


Figure 3.4 Interaction plot for tibial growth (mm/week) showing the dependence of temperature and altitude.

3.4 Discussion

It is known that some species exhibit sexual dimorphism, however, *Hemideina* are unusual in that males of this genus may exhibit trimorphism and become sexually mature at the eighth, ninth or tenth instar (Kelly, 2008b; Kelly & Adams, 2010; Spencer, 1995). Although no males in this study were seen to become sexually mature at the eighth instar, ninth instar maturation was seen as often as maturation at tenth instar in those males that did reach sexual maturity in this study. Three-quarters of early maturing males were *Hemideina crassidens* and 86% came from the Palmerston North population. This is not different from the random distribution of early maturing males as would be seen in the wild population according to species and location. Sexual selection is well studied in *Hemideina* sp, with males using their enlarged mandibles to actively defend a harem of females and mating with them within the roost cavity (Kelly, 2005, 2008a; Kelly & Adams, 2010; Leisnham & Jamieson, 2004). This may drive sexual maturity at a smaller size, allowing smaller 'sneaker' males to mate with females within a harem of a larger male under the guise of a female and to gain access to roost holes where the large heads of the tenth instar males prevent access (Kelly & Adams, 2010).

In this study as in others (Spencer, 1995), two quantitative measures of growth were used: allometric growth that occurs in limbs during moulting of hemimetabolous insects gives a view of size at any time after hardening of the cuticle; whereas total growth measured in mass (weight) will increase during an instar and perhaps drop off just before a moult as feeding ceases, giving a less accurate analysis of size at any one time, but a more comprehensive analysis of growth overall. Whether measured allometrically or by weight, tree weta in this study show consistency in their growth and all treatment groups showed significant differences at the same points in both weight and tibial growth. This suggests that perhaps one measure of size is not better than the other overall, but, either weight or length characteristics will give an indication of both growth rate and life stage for any given *Hemideina* individual. This study does show that generally, *Hemideina crassidens* are heavier than *H. thoracica*, but *H. thoracica* has a longer mean tibia length.

Sizes at instars were similar to those in Spencer (1995), although this study showed smaller tibia lengths in males at instars eight and nine although this may be due to separation of early maturing males from tenth instar males in this study. Additionally, there is no separation between the size of early maturing males and males at eighth instar which suggests that perhaps it is only in the late stage of the eighth instar that early maturation is determined, possibly due to external cues such as environment or due to delayed intrinsic cues. Tree weta from Mt Taranaki show greater weights and tibia lengths at instar nine and ten than those from Palmerston North which fits with theories that there is an increase in size of ectotherms with an increase in altitude (Atkinson, 1994; Bidau & Marti, 2008), despite only *H. thoracica* showing a positive increase in size with temperature (2.3.3, this thesis). There appears to be some variation in sizes between *Hemideina crassidens* and *H. thoracica* with *H. crassidens* being heavier at the later instars.

Allometric growth in hemimetabolous insects is said to adhere to a linear relationship, increasing in size by a specific ratio each moult (Whitman, 2008) which varies between orders and appendages. The tree weta studied here appear to conform to this rule in tibia length by increasing by a ratio of 1.14 in early maturing males, 1.19 in males and 1.13 in females. This also occurs in Spencer (1995) who looked at numerous appendages but found only tibial and femoral growth to be consistent. This may be unusual, as Orthoptera do not appear to readily conform to scaling models (Whitman, 2008). Perhaps tibial growth in *Hemideina* sp is linear as there is no physiological change in relation to the growth of tibia in tree weta as there is with femoral length, i.e. increased ability to jump with increased size. This, however, allows us to meet the assumptions required in the statistical analyses performed.

Because *H. crassidens* and *H. thoracica* have quite discrete ranges we expected physiological differences might be revealed when we compared growth rates. It is surprising, therefore, that none of the variation in growth rates observed could be attributed to species differences. Striking differences in growth rate are seen when the high altitude populations (from Taranaki) are compared to the low altitude populations (Palmerston North) and there is no interaction between location and species. At both temperatures (9^{o}C

and 14°C) the weta from high altitude populations grew faster than the weta from the low altitude populations, although the difference was more pronounced at 14°C. This faster growth resulted in larger adults for both *H. crassidens* and *H. thoracica*.

This suggests a genetic difference between the two populations of *Hemideina crassidens* and *H. thoracica* that allows for a faster rate of growth during what is likely to be a shorter growing season at high altitude. Berner, et al. (2004) showed a similar response to altitude in *Omocestus viridulus* (Acrididae) with high altitude populations showing a higher rate of growth and attaining sexual maturity faster than those from a lower altitude when raised in a common environment. This contradicts theories by Davidowitz & Nijhout (2004) who suggested that ectotherms in a colder climate are more likely to be influenced by the growing period and therefore take longer to reach adult size than those in warmer climates that have a final body size determined by growth rate. Chapter 2.3.3 (this thesis) considers that, at least in *H. crassidens*, there is no relationship between body size and temperature therefore not conforming to a Bergmannian size cline. Perhaps the final size of tree weta from colder climates is dictated by growing season (as in Davidowitz & Nijhout, 2004) but as a result of that, reaches a smaller mature size due to a shorter optimal growing period. The grasshopper *Melanoplus sanguinipes* also shows a higher growth rate and lower mature body mass in individuals taken from a colder climate (Alaska, sub-arctic) than those from the temperate region of Idaho regardless of what temperature they were raised at (22°C, 30°C or 33°C) (Fielding & Defoliart, 2007), which may be due to the shorter growing season in Alaska (106 growing days vs. 187 days). This is thought to come at a cost of sensitivity to a poorer quality diet which leads to increased consumption and therefore a greater proportion of time feeding in colder climates, which may lead to a greater chance of predation and could be seen as a reduction in fitness (Fielding & Defoliart, 2007).

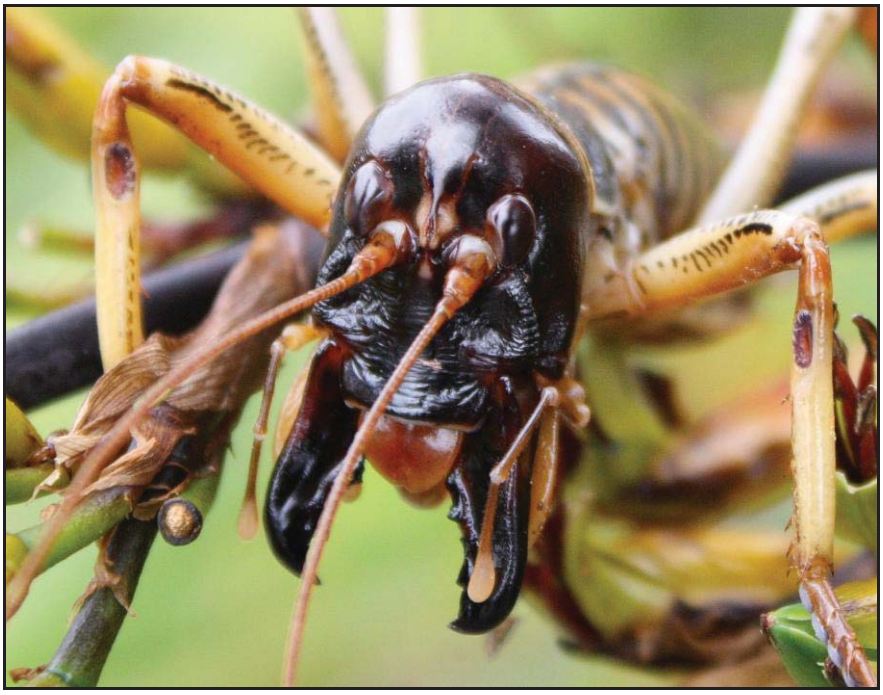
The two species have sex-associated differences in their growth rate, with early-maturing males of *H. crassidens* having a much higher growth rate than *H. thoracica*. In both species, females show the highest rate of growth, but in *H. crassidens*, early maturing males show a faster growth rate than males. Female tree weta of both species have a greater rate of growth than males despite similar tibia lengths and weights between sexes at maturity.

This fits with the theory that a male tree weta will trade off lifespan for the increased mating opportunities (Zajitschek, Bonduriansky, Zajitschek, & Brooks, 2009) that come with a larger head size (sexual dimorphism) (Kelly, 2005, 2008a; Leisnham & Jamieson, 2004). Thus males will have a slower growth rate that although leads to them reaching the same tibial and weight size as females, allows for greater somatic investment in a larger head size (Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008; Kelly, 2005; Maklakov, Bonduriansky, & Brooks, 2009).

3.5 Conclusions

Grown under constant conditions the high-altitude populations of both weta species were larger as adults than their conspecifics from low-altitude populations. This size difference resulted from a clear difference in growth rate; the high-altitude populations of both species grew faster at both 9^{o}C and 14^{o}C. The strongest evidence for differences in growth rate between treatments of tree weta comes from a pairing of population and temperature. Such significant differences between low and high altitude populations regardless of species suggest profound physiological variation between the groups. It is suggested that physiological adaptations to altitude come in the form of shifts in enzymes kinetics, membrane fluidity and metabolism (Kingsolver & Huey, 1998) and that life history theory predicts this counter-gradient variation to have arisen from natural selection.

4 Oxygen Consumption of Two Tree Weta Species, Measured by Closed Circuit Respirometry.



4.1 Introduction

Parapatric species are those that share a separate yet continuous distribution in the absence of any physical barriers (Garcia-Ramos, et al., 2000). This type of distribution could be maintained by competitive exclusion or, if resources are plentiful, an environmental gradient that constrains one or both populations to a physiological limit that may exclude one species from another's habitat (Garcia-Ramos, et al., 2000; Gaston, 2009). Where there is an environmental gradient, the steeper the gradient the more defined the boundary between the two species is likely to be. As the climate changes (or the environment is modified), so the distribution of the populations may shift to optimise physiological adaptations (Gaston, 2009).

Physiologically, there are many factors that can limit alpine insect populations. Air temperature can vary up to 6.5°C per 1000 metres, partial pressure of oxygen decreases with an increase in altitude, precipitation increases with altitude, solar radiation is greater at higher altitude (Dillon, et al., 2006; Hodkinson, 2005) and wind speed increases with altitude (Hodkinson, 2005) in a similar fashion to the changes seen in the environmental conditions with increasing or decreasing latitude (northern hemisphere/southern hemisphere). Although the effects on populations with an increase in altitude are comparable with a change in latitude, the magnitude is somewhat different. Whilst there may be a large change in gradient over several vertical (altitudinal) kilometres, it may take many hundreds of kilometres to achieve a similar change in gradient over a horizontal (latitudinal) platform (Hodkinson, 2005) meaning that the alpine system will comparatively have a much steeper environmental gradient, and thus a narrow and defined boundary between two parapatric species.

Of the many environmental variables, it is the low oxygen partial pressure (pO_2) which appears to have the greatest bearing on the alpine communities, but this in turn is influenced strongly by air temperature (Dillon, et al., 2006). With air temperature dropping in an inversely proportional fashion as altitude is gained, partial pressure of oxygen also reduces (Dillon, et al., 2006). As a result, adaptations to unfavourable climatic conditions

are required to continue the survival of an alpine population. This may involve either behavioural or physiological changes in the overall population or the individual animal. Behaviourally, insects may induce torpor to slow down metabolic rate and essentially 'sleep' away the winter months and grow, mate and breed in the more favourable summer months, such as seen in the alpine scree weta, *Hemideina maori*, of Southland, New Zealand (Joyce, Jamieson, & Barker, 2004; Sinclair, et al., 1999). Alternatively, insects may also migrate to warmer climates as seen in the Lepidoptera: Noctuidae (Feng, Wu, Wu, & Wu, 2009), Nymphalidae (Froy, Gotter, Casselman, & Reppert, 2003) and Yponomeutidae (Campos, Schoereder, & DeSouza, 2006). Flightless insects, however, are somewhat restricted to enduring winter conditions.

There are two strategies for over-wintering in freezing temperatures: freeze tolerance and freeze avoidance/freeze intolerance (Bale, 2002; Somme, 1999). Freeze tolerant insects begin producing ice nucleating proteins (INAs), anti-freeze proteins (AFPs) and polyols and sugars in the autumn when temperatures begin to fall. These compounds move water out of cells to prevent cell damage from ice nucleation as well as prevent secondary ice crystallisation as temperatures rise following winter. This allows the insect body to cool to as low as -80°C (Bale, 2002). Insects that employ freeze avoidance do so by allowing their bodies to 'supercool'. This is initially behavioural, involving the removal of excess water from the body, evacuation of faecal matter and cessation of feeding. Secondly, supercooling insects also produce cryoprotectant compounds such as polyols and AFPs that allow the supercooling point to lower to as much as -20°C (Bale, 2002). Metabolic rate is also involved in prevention of freezing. By increasing metabolic rate, a greater temperature is produced and the more active an animal may be in colder environments.

Metabolic cold adaptation (MCA) refers to the ability of an individual or population to survive temperatures below the normal minimum threshold for survival, due to the evolution of physiological changes allowing the animal to adapt to low environmental temperatures (Addo-Bediako, Chown, & Gaston, 2002). This is seen as an increase in the metabolism of cold adapted animals when compared to the same or similar species from a warmer climate (Addo-Bediako, et al., 2002; Massion, 1983). This phenomenon has

previously been shown in several orthopteran families: Gryllidae (Booth & Kiddell, 2007) and Acrididae (Chappell, 1983; Massion, 1983).

Metabolism is the basis of survival and growth for all living creatures. Through catabolism, animals are able to grow and reproduce while anabolism allows an animal to actively seek out food and shelter and to increase their fitness. An increased metabolic rate in animals from a cooler climate allows them to balance out the increased ATP demand from living in an environment that has a relatively cooler and shorter growing season (Addo-Bediako, et al., 2002; Oikawa, Mori, & Kimura, 2006). Elevated metabolic rates are rarely seen outside of specifically required areas i.e. cold environments, as there is a fitness cost associated with a higher metabolic rate (Addo-Bediako, et al., 2002; Conover & Present, 1990). Therefore, a population with an adaptation such as MCA can be constrained to a narrow climate range which may influence distribution of that species.

Many studies have been completed on the alpine 'tree' weta *Hemideina maori* found in the Southern alps (Joyce, et al., 2004; Neufeld & Leader, 1998; Ramlov, 1999; Rock, Cook, Murray, Thomas, & Jamieson, 2002; Sinclair & Wharton, 1997; Sinclair, et al., 1999), however, other tree weta species (*Hemideina crassidens* and *H. thoracica*) are known to inhabit high altitudes on mountains of the North Island. Mt Taranaki in particular shows strong parapatry between these two species with *Hemideina crassidens* found on the higher altitudes of the mountain (exclusive above 1000 m (Jacobson, 2009; Trewick & Morgan-Richards, 1995)) surrounded by *H. thoracica* at lower levels (exclusive below 800m (Jacobson, 2009; Trewick & Morgan-Richards, 1995)). These parapatric species appear to competitively exclude each other (Trewick & Morgan-Richards, 1995). The ability of tree weta to survive (and competitively exclude a congeneric species) in a high altitude habitat and the absence of any hybrid forms at this boundary (Trewick & Morgan-Richards, 1995) suggests that the species are reproductively isolated, and that competitive exclusion by physiological adaptations such as metabolic cold adaptation might operate. As the high latitude species (further from the equator) it is likely that *H. crassidens* is better adapted to colder climates than *H. thoracica*, as seen by their distribution on the higher altitudes of Mt Taranaki, Mt Ruapehu and into South Island, New Zealand (2.3.1, this thesis). The

hypothesis I tested was that metabolic cold adaptation provides *H. crassidens* with a higher metabolic rate allowing this species to survive and competitively exclude *H. thoracica* on Mt Taranaki. In order to test this hypothesis a comparison of measured metabolic rate (MR) of the two species was required. Metabolic rate can be estimated by the rate of oxygen (O_2) metabolism. This is the simplest method resulting in an almost exact correlation to MR due to the amount of heat being produced per litre of O_2 consumed in metabolism being constant regardless of whether it is fat, protein or carbohydrate being metabolised (Schmidt-Nielsen, 1998). I predict that high altitude populations will have a higher rate of oxygen consumption than those from low altitude populations and *H. crassidens* from Mt. Taranaki will have a higher rate of oxygen consumption than *H. thoracica* from Mt. Taranaki giving them a competitive advantage to living in colder climates.

4.2 Methods

4.2.1 Study animals

The animals used in these experiments were New Zealand tree weta (Orthoptera: Anostostomatidae) consisting of *H. thoracica* (Auckland tree weta) and *H. crassidens* (Wellington tree weta) collected from lowland and high-altitude locations. To represent lowland individuals, both species of weta were collected over the summer of 2009-2010 from the Kahuterawa Valley, Manawatu, New Zealand (150 m asl) by hand collecting during daylight. Additional *H. thoracica* were collected by the same method from the Waiopehu Reserve, Horowhenua, New Zealand. Mount Taranaki weta were collected from Manaia, Egmont and Pembroke Roads and Wilkies Pools Loop track between March and November 2010 by hand collecting and from previously positioned artificial roosts.

All weta used were adults to avoid the effects of a changing VO_2 seen in juvenile orthopteran instars (Booth & Kiddell, 2007; Rowe, 2009) and all female weta were raised in the lab from juveniles to ensure they were not mated and therefore changes in VO_2 with oogenesis might be reduced. Sexually mature tree weta (adults) were distinguished by morphological characteristics of sharp, curved, shaded ovipositors in females and by curved cerci in males (M. Morgan-Richards, personal communication. February 10th 2010). Any

irresolute individuals were tested for sexual behaviour against known adults of the opposite sex (Spencer, 1995).

Animals were kept individually in 2L containers with wire mesh fitted into the lids to allow ventilation and furnished with lengths of hollowed flax (*Phormium* sp.) flower-poles as roost holes. All weta were initially kept at a 12:12 light dark cycle that was gradually extended to a 14:10 light dark cycle with the approach of summer. The weta were allowed ad libitum access to foliage of *Coprosma* sp., *Melicytus ramiflorus* (Mahoe, whiteywood) and *Prumnopitys ferruginea* (Miro, brown pine); the seasonal fruits of the afore mentioned plants and carrot. Each weta box also contained a damp square of paper towelling to provide moisture. The weta diets were supplemented weekly with soya protein (Thompson's Red 8 Protein Plus 80% nuggets).

At 6°C, a total of 46 adult tree weta were tested (Table 4.1) and at 14°C, a total of 58 adult tree weta were tested (Table 4.2). Forty-two adult tree weta were used in both 14°C and 6°C trials (see appendix).

Table 4.1 Number of tree weta in 6°C treatment group (see appendix).

	Male	**Female**	**Total**
Hemideina crassidens	13	14	27
Hemideina thoracica	5	14	19
Palmerston North	11	19	30
Mount Taranaki	7	9	16

Table 4.2 Number of tree weta in 14°C treatment group (see appendix).

	Male	Female	Total
Hemideina crassidens	17	14	31
Hemideina thoracica	9	18	27
Palmerston North	15	23	38
Mount Taranaki	11	9	20

4.2.2 Treatments

4.2.2.1 Determination of Lower Temperature Limits

Initially, we performed activity vs. temperature tests to establish the lower threshold of temperature in which activity was still observed.

Weta were kept in the aforementioned housing and at the beginning of the experiment, were placed inside the roost with a strand of hair placed across the exit. In this way, we could detect when the weta left its roost. Additionally, a single *Coprosma repens* leaf was placed away from the exit of the roost to test for feeding. Weta were kept at constant temperatures in a temperature controlled room for five days at a time and checked daily for roost exiting and/or feeding. If the hair was disturbed or the foliage was eaten, the study was reset to detect activity over the following 24 hours. For each 5 day period, weta were tested at 1°C intervals between 8°C and 5°C.

4.2.2.2 Oxygen Consumption

Oxygen consumption was measured at both 14ºC and 6ºC to simulate a seasonal change in temperature. All tests were performed within temperature controlled rooms to ensure constant temperatures. Before experimentation, the weta were allowed to acclimatise to the study temperature for ten days and all weta used were starved for 24 hours prior to use in

this study to remove potentially complicating digestive effects. Once the software was calibrated and *k* established (4.2.4, this thesis), a single weta was placed in an open ended glass tube covered with dark plastic to simulate darkness and stimulate resting by reproducing a natural roosting space which is essential to remove any chance of anaerobic metabolism (Schmidt-Nielsen, 1998). The open end of the tube was closed with the recording probe inserted into a rubber bung to ensure an air-tight seal. Once the weta began resting, the recordings began. The data were collected for approximately 3 hours or until a 3% drop in partial pressure of oxygen (pO_2) was observed (C. Rowe, personal communication, September 21st, 2009). The Stern-Volmer equation was used to calculate oxygen partial pressures (see 4.2.4 Calculations).

4.2.3 Respirometry

A closed circuit respirometry system was chosen for this study due to the size of the animals and the relative simplicity and inexpensiveness of the setup. The program used to record the oxygen metabolism was OOISensor ver. 1.05, OceanOptics Inc., USA. This system uses an LED light (approximately 475 nm) in an optical fibre which excites a sol-gel formulation at the tip to fluoresce at approximately 600 nm. When this complex encounters an oxygen molecule, the excess energy quenches the fluorescent signal giving a reading that correlates with the partial pressure of oxygen within the chamber. This "oxygen lifetime" can then be transformed into pO_2 using the Stern-Volmer equation (Carraway, Demas, Degraff, & Bacon, 1991).

The program was first calibrated at each temperature with gas containing a high pO_2 (air ≈ 20.95% oxygen) and low pO_2 (100% nitrogen gas ≈ 0% oxygen). These lifetime standards were then used to calculate the Stern-Volmer constant (*k*).

4.2.4 Calculations

4.2.4.1 Stern-Volmer calculations

Stern-Volmer equation: $T_0/T = 1+k\ pO_2$

Where T_0 = lifetime in 0% O_2

T = lifetime in variable O_2

To calculate *k*, T_0/T can be plotted against pO_2 to give a linear graph, the slope of which is equal to *k* (Figure 4.1 and Figure 4.2).

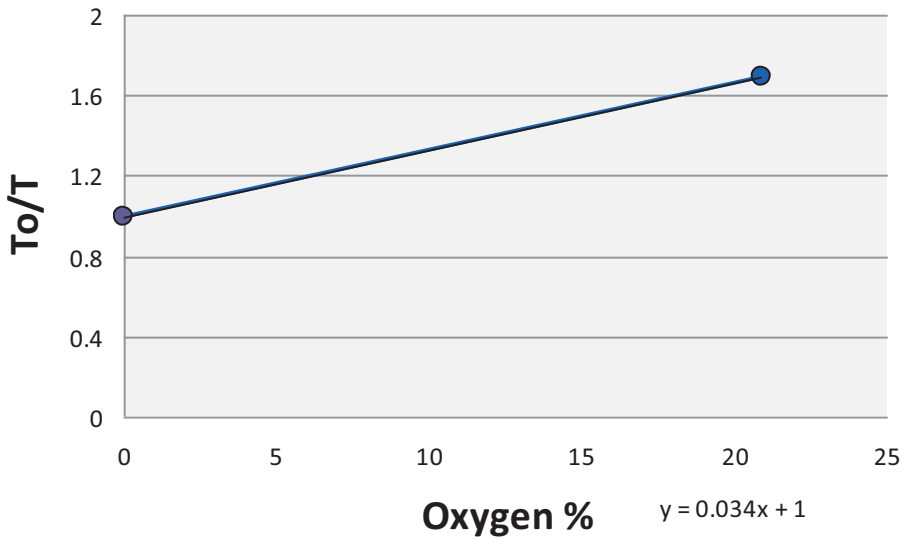


Figure 4.1. Calculation of constant *k* at 14°C resulting in a value of 0.034.

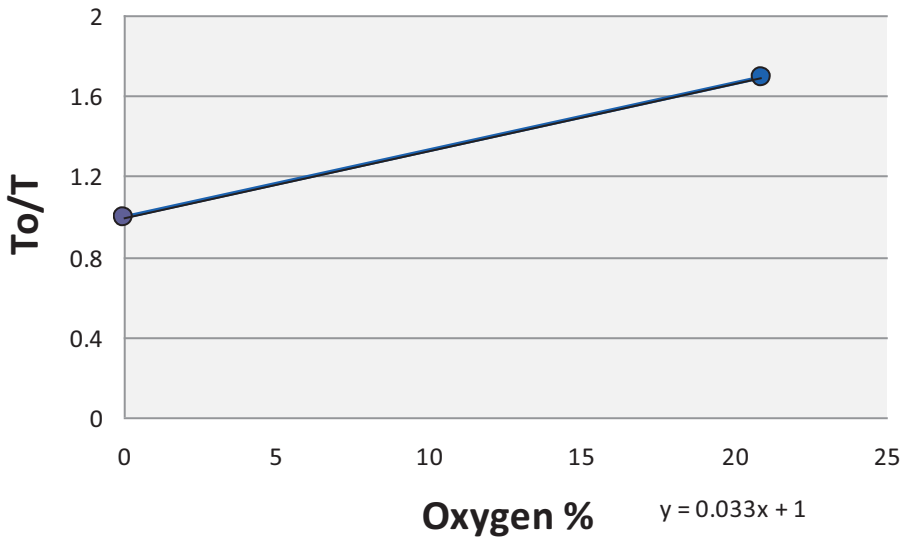


Figure 4.2. Calculation of constant *k* at 6°C resulting in a value of 0.033.

$$T_0/T = 1+k\,pO_2$$

When rearranged:

$pO_2 = (T_0/T)-1/k$

With initial and final pO_2 calculated, then the change in pO_2 can be calculated to ensure that at least a 3% drop in pO_2 has occurred.

4.2.4.2 Oxygen consumption calculations

To convert pO_2 to the rate of oxygen metabolism (VO_2) the following equation may be used:

$$VO_2=V(f_i-f_f)/(1-f_f)t$$ (Nespolo, Lardies, & Bozinovic, 2003)

Where V = volume of chamber (ml)

f_i = Initial pO_2

f_f = final pO_2

t = time (hours)

Finally, VO_2 is tested to take into consideration the mass of individual animals (Figure 4.3, Figure 4.4 and Figure 4.5). If desired, this can be converted to metabolic rate by multiplying by 20.1 (Schmidt-Nielsen, 1998) i.e. the number of joules per 1ml of O_2 (Hack, 1997).

4.3 Results

4.3.1 Determination of Lower Temperature Limits

The lower temperature limit of activity for both species of tree weta was determined by testing for feeding and emergence from the roost at various temperatures (Table 4.3). At 5°C, although a small number of weta emerged from the roost, no feeding activity was recorded. At 6°C a greater number of tree weta emerged from the roost and a small number were recorded as having consumed some foliage. From this I infer that *Hemideina crassidens* and *H. thoracica* have a lower activity limit of approximately 6°C.

Table 4.3. Examining the lower temperature limits still conducive to activity in *Hemideina crassidens* and *H. thoracica.*

	% of time activity observed	
Temperature (total number of observations)	**Emerged**	**Foliage consumed**
5°C (31)	3.32	0
6°C (39)	10.26	2.56
7°C (71)	22.54	16.9
8°C (15)	33.33	20.0

4.4 Mass specificity

The mean weight of all adult *Hemideina crassidens* used in this study was 4.48g, significantly greater than *H. thoracica* at 3.99 g ($P = 0.013$, two sample t-test). Adult weta from the two Mt. Taranaki populations were on average significantly heavier than adults from Palmerston North (4.97 g and 3.87 g) ($P < 0.001$, two sample t-test). Weights in females are likely to be influenced by the number of eggs they have produced and body condition (Griffin, Morgan-Richards, et al., 2011), and the weight of an adult male will vary depending on instar and body condition (Spencer, 1995). However, species and population differences are also likely (see chapter 3).

Mass specificity was tested to ensure uniformity in statistical examinations. At 6°C, a plot of mass against VO_2 gave a non-significant R^2 value of 0.023 ($P = 0.374$). At 14°C, a plot of mass against VO_2 gave a significant R^2 value of 0.196 ($P < 0.001$). This indicates a positive correlation between mass and oxygen consumption at 14°C (Figure 4.3) although not at 6°C (Figure 4.4). A regression between the combined mass and oxygen consumption of both species failed to show a correlation (Figure 4.5) between the variables (oxygen consumption= 0.774-0.0252 mass, R^2= 0.0%, P= 0.471). Because of the differences in mass correlation between the two temperatures but also the significant differences in VO_2 seen between them, the data were analysed both with and without mass specificity.

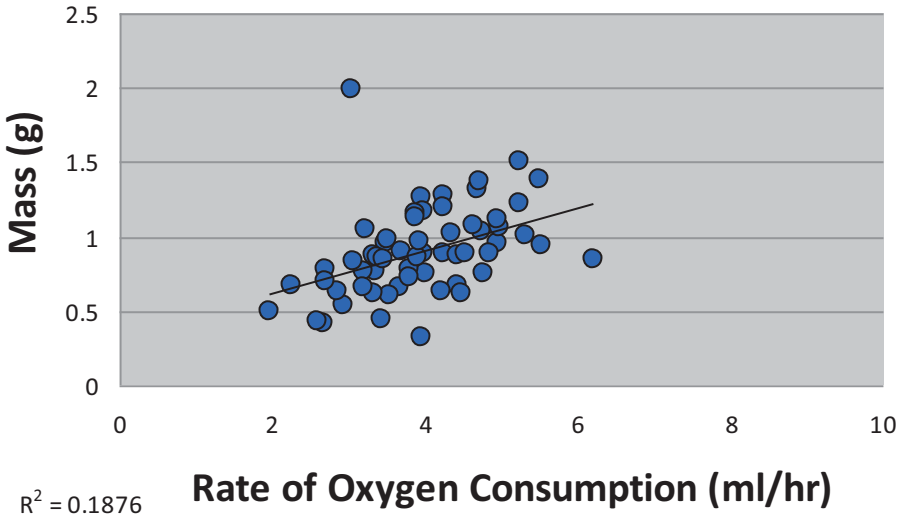


Figure 4.3. Correlation between the size of the weta (weight) and estimated oxygen consumption, with 19% of the oxygen consumption at 14°C explained by mass.

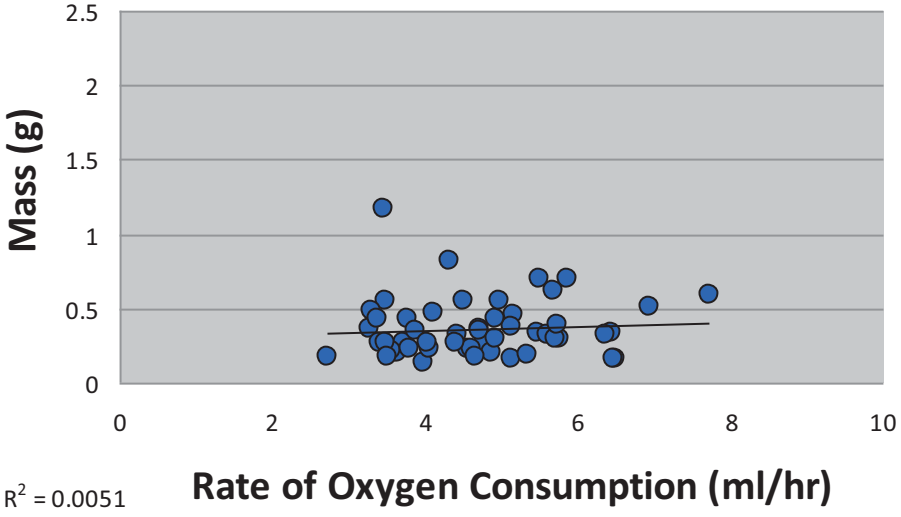


Figure 4.4. Little correlation is seen between the size of the weta (weight) and estimated oxygen consumption, with only 0.5% of the oxygen consumption at 6°C explained by mass.

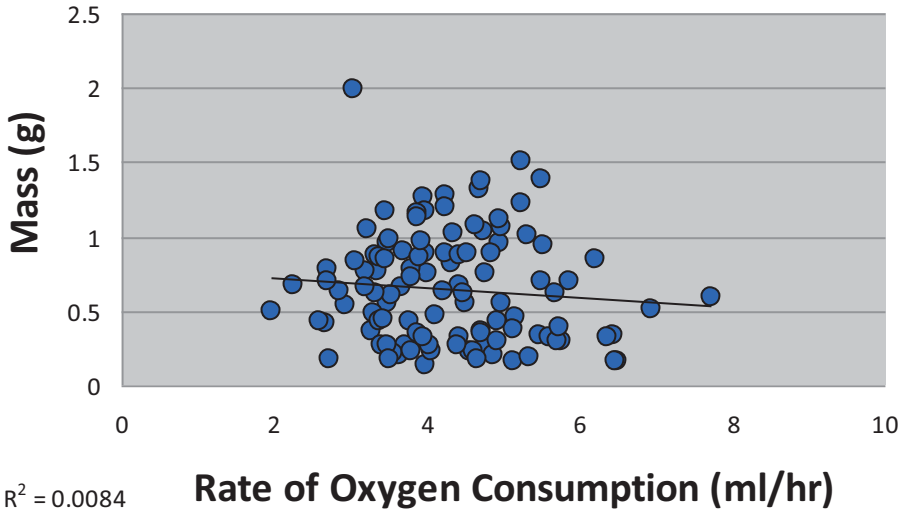


Figure 4.5 No significant correlation is seen between rate of oxygen consumption and mass in tree weta as 0.8% of oxygen consumption is explained by mass when 6°C and 14°C data are combined.

4.4.1 Oxygen Consumption of Tree Weta

4.4.1.1 Non-Mass Specific Oxygen Consumption

Due to non-normal distribution of all metabolic data, non-parametric tests were used.

Individual weta had a higher mass specific oxygen consumption at 14°C compared to 6°C but individual weta with high consumption at 14°C did not show a comparatively high consumption at 6°C (Figure 4.6). In fact one weta produced almost the same oxygen consumption rate at 6°C as at 14°C and two weta showed higher oxygen consumption rates at 6°C than at 14°C.

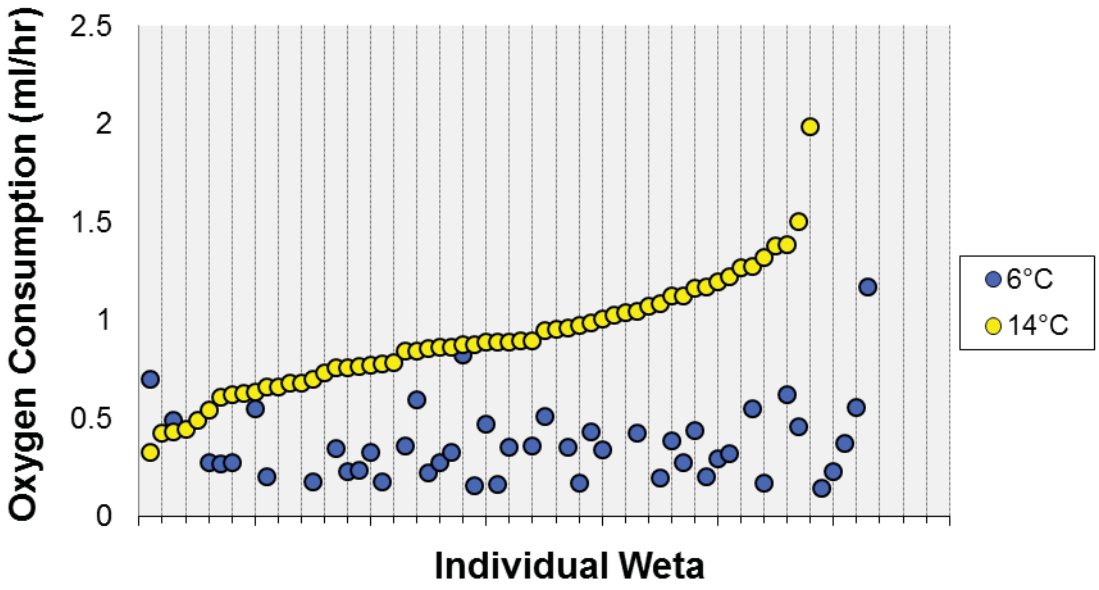


Figure 4.6 Comparison of oxygen consumption in individual weta tested at 6°C and 14°C

No differences in medians were found between sex (male vs. female), species (*Hemideina crassidens* vs. *Hemideina thoracica*) or populations (Palmerston North vs. Mount Taranaki) (Kruskal-Wallis test of medians, P = 0.932, 0.435 and 0.131 respectively) (Figure 4.7). However, temperature does show a significant difference ($P < 0.001$, DF=1) (Figure 4.8) with the rate of specific oxygen consumption being 3.4 times higher when weta were tested at 14°C than at 6°C.

When the temperature treatments were separated and re-tested with a Kruskal-Wallis test, neither 6°C nor 14°C showed significant differences in medians of sex, species or population (6°C P = 0.839, 0.780 and 0.174 and 14°C P = 0.254, 0.950 and 0.025 respectively).

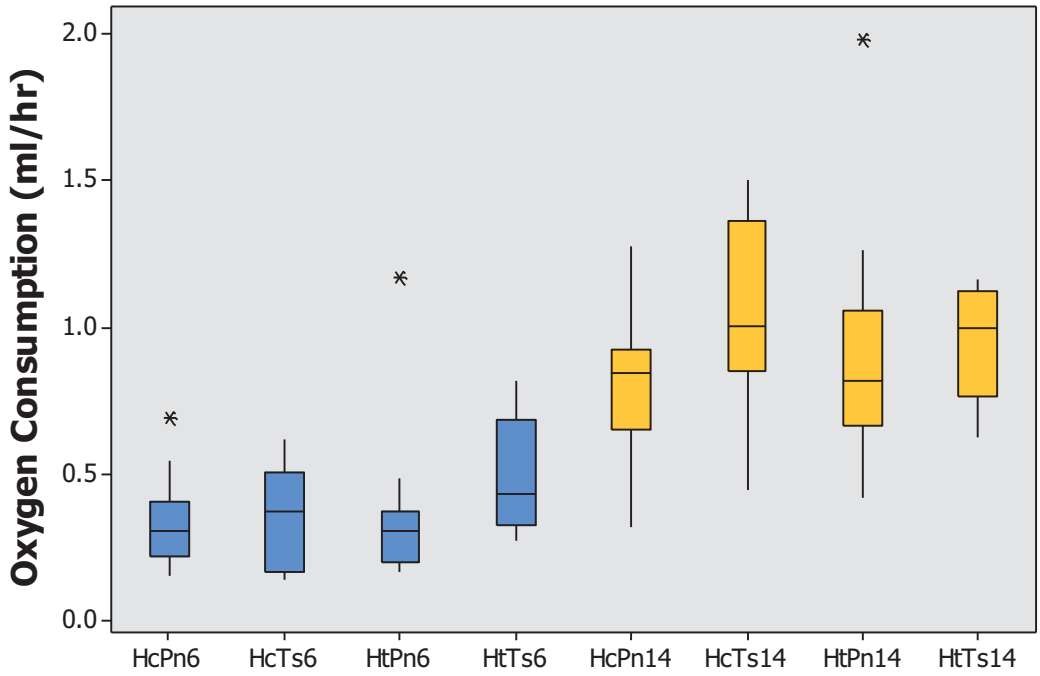


Figure 4.7 Treatment groups and their rates of oxygen consumption. X-axis abbreviations; Hc: *Hemideina crassidens*, Ht: *Hemideina thoracica*, Pn: Palmerston North (lowland) population, Ts: Mount Taranaki (high altitude) population, 14: 14°C and 6: 6°C.

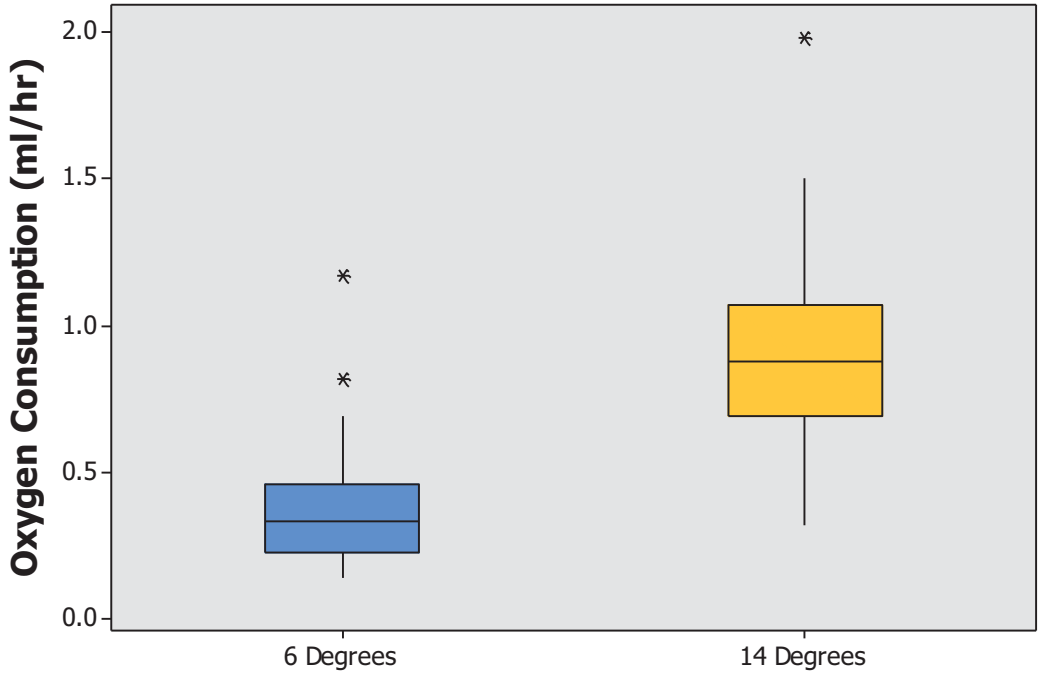


Figure 4.8 Significant differences in oxygen consumption between 6°C (median=0.3342ml/hr) and 14°C (median=0.9790 ml/hr).

4.4.1.2 Mass Specific Oxygen Consumption

Due to non-normal distribution of all metabolic data, non-parametric tests were used.

Individual weta had a higher mass specific oxygen consumption at 14°C compared to 6°C. With the exception of a single outlier, individual weta with high mass specific oxygen consumption at 6°C do not also have a comparatively high consumption at 14°C (Figure 4.9). No differences in medians were found between sex (male vs. female), species (*Hemideina crassidens* vs. *Hemideina thoracica*) or populations (Palmerston North vs. Mount Taranaki) (Kruskal-Wallis test of medians, P = 0.261, 0.181 and 0.460 respectively). However, temperature does show a significant difference ($P < 0.001$, DF=1) (Figure 4.10 and Figure 4.11) with the rate of mass specific oxygen consumption being 3.4 times higher when weta were tested at 14°C than at 6°C.

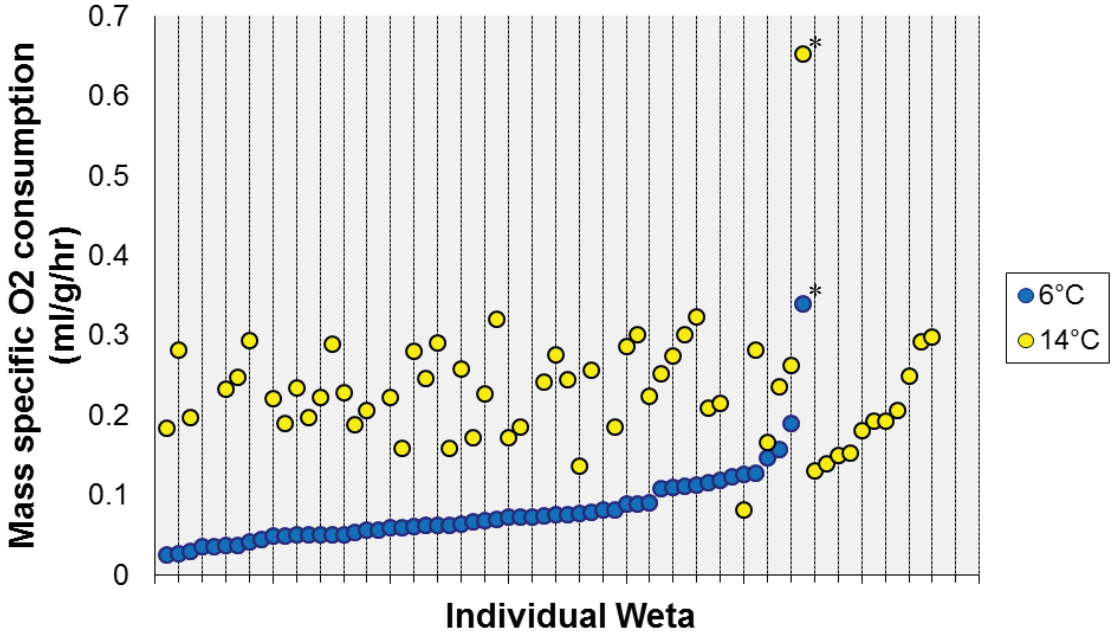


Figure 4.9 Comparison of mass specific oxygen consumption (MSOC) in individual weta tested at 6°C and 14°C. The outlier (*) is a true measurement as repeated measurements consistently achieved high mass specific VO_2.

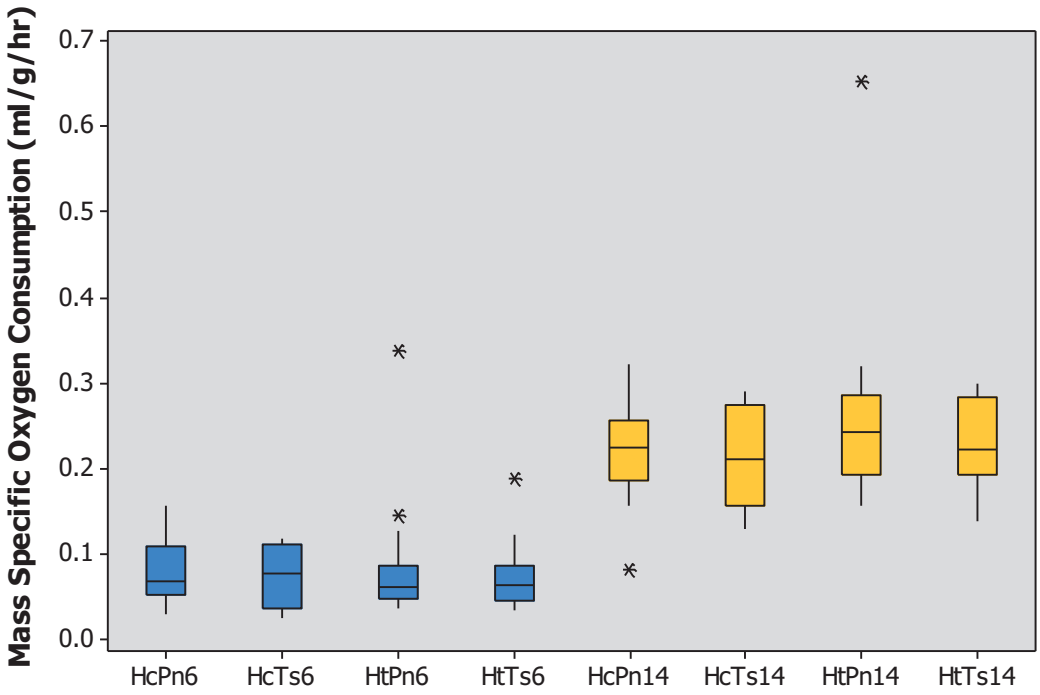


Figure 4.10 Treatment groups and their rates of mass specific oxygen consumption. X-axis abbreviations; Hc: *Hemideina crassidens*, Ht: *Hemideina thoracica*, Pn: Palmerston North (lowland) population, Ts: Mount Taranaki (high altitude) population, 14: 14°C and 6: 6°C.

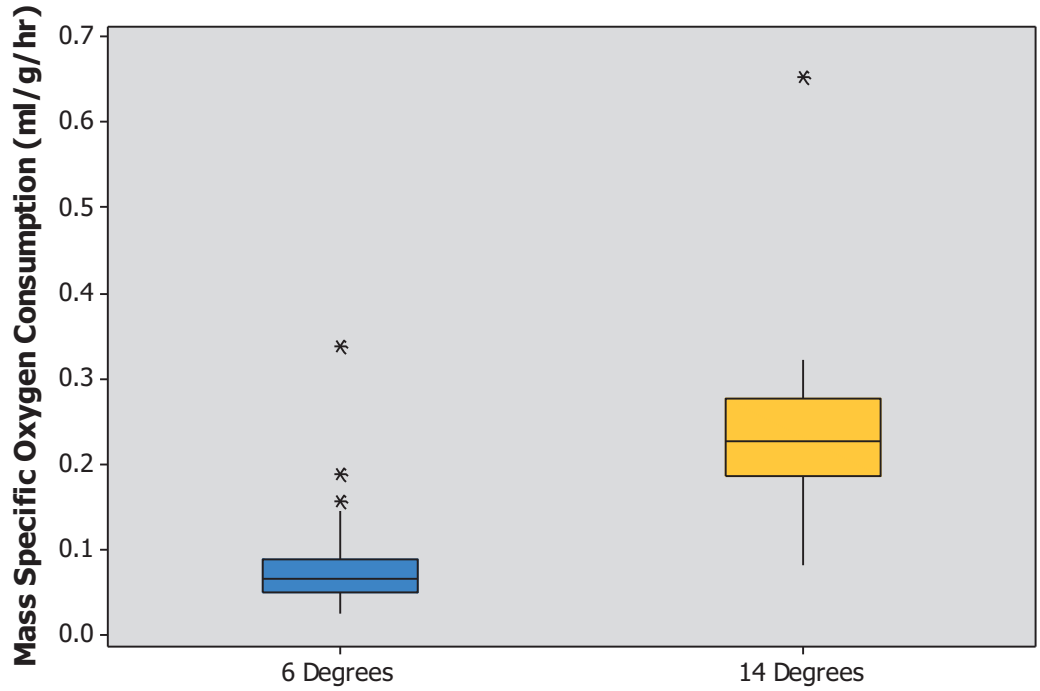


Figure 4.11 Significant differences in mass specific oxygen consumption between 6°C (median=0.07016) and 14 °C (median=0.21741).

When the temperature treatments were separated and re-tested with a Kruskal-Wallis test, neither 6°C nor 14°C showed significant differences in medians of sex, species or population (6°C P = 0.180, 0.986 and 0.649 and 14°C P = 0.282, 0.191 and 0.360 respectively).

4.5 Discussion

The two species of tree weta studied here appear to show a positive correlation between mass and oxygen consumption at 14°C but not at 6°C, although many individual weta were used in both experiments (see appendix). However, mass specific oxygen consumption was similar to that recorded in other insects at similar temperatures such as *Hophlosphyrum griseus* (Ensifera) (Table 4.4). *Hemideina crassidens* had a mean rate of 0.08 ml/g/hr at 6°C and 0.22 at 14°C and *H. thoracica* had a mean rate of 0.14 ml/g/hr at 6°C and 0.25 ml/g/hr at 14°C. Both tree weta species combined showed a range of rates between 0.025 ml/g/hr (6°C) and 0.653 ml/g/hr (14°C).

This study showed no positive correlation in combined temperature studies between mass and oxygen consumption unlike other Orthoptera studies (Ashby, 1997; Booth & Kiddell, 2007; Nespolo, et al., 2003; Terblanche, Clusella-Trullas, Deere, Van Vuuren, & Chown, 2009) and contrary to the proposed hypothesis, this experiment has been unable to show that high altitude tree weta have a higher VO_2 (whether mass specific or not) when tested at the same ambient temperature as lowland tree weta, or that *Hemideina crassidens* has a higher VO_2 than *H. thoracica*. Nonetheless, it did show that most individual tree weta will exhibit a higher VO_2 at elevated temperatures than at cooler temperatures (Table 4.4). This positive correlation is unsurprising as it is well known that chemical reactions take place at a faster rate with increasing temperature as described by the Van't Hoff effect (Booth & Kiddell, 2007), hence the increase in oxygen consumption at higher temperatures to fuel an increased rate of cellular metabolism. This has been reported in other Orthoptera such as in Chappell (1983), when Acrididae showed an increase in VO_2 with temperature in populations found in both alpine habitat (3800 m asl, *Melanoplus*

Table 4.4 Comparison of methods and results in mass specific oxygen consumption studies of Orthoptera. [1]Figure calculated from standard metabolic rate and mean weight for species. [2]In this study elevation is represented by acclimation temperatures 25°C, 29°C and 33°C. [3]Based on oxygen consumption measured as carbon dioxide release.

Species	System	Mass specific VO_2 (ml/g/hr)	Mass specific VO_2 change with elevation	Reference
Hemideina crassidens (Anostostomatidae)	Closed	0.08436 @ 6°C 0.22063 @ 14°C	Neutral	This study
Hemideina thoracica (Anostostomatidae)	Closed	0.13613 @ 6°C 0.24459 @ 14°C	Neutral	This study
Xanthippus corallipes (Acrididae)	Closed	1.29225 @ 35°C 2.296916 @ 45°C	Neutral	(Ashby, 1997)
Archeta domesticus (Gryllidae)	Closed	2.01639 @ 25°C 2.5208 @ 28°C	N/A	(Booth & Kiddell, 2007)
Trimerotropis pallidipennis (Acrididae) (low land) *Melanoplus sanguinpes* (Acrididae) (alpine)	Closed	4.32289[1] (mean daily temperature) 7.083227[1] (mean daily temperature)	+	(Chappell, 1983)
Hophlosphyrum griseus (mogoplistidae)	closed	0.0799 @ 7°C 0.2130 @ 17°C 0.4735 @ 27°C	+	(Hack, 1997; Nespolo, et al., 2003)
Aeropedellus clavatus (Acrididae)	Flow through	N/A	+	(Hadley & Massion, 1985)
Archeta domesticus (Gryllidae)	Flow through	N/A	+[2]	(Lachenicht, Clusella-Trullas, Boardman, Le Roux, & Terblanche, 2010)
Trimerotropis pallidipennis (Acrididae) 2300 masl *Trimerotropis suffusa* (Acrididae) 3900 masl	Closed	1.3584 @ 40°C 2.3664 @ 40°C	+	(Massion, 1983)
Melanoplus sanguinipes (Acrididae) 500 masl and 3123 masl	Flow through	N/A	+[3]	(Rourke, 2000)

sanguinipe) and desert habitat (250 m asl, *Trimerotropis pallidipennis*) (Table 4.4). Ashby (1997) also tested six populations of *Xanthippus corallipe* (Acrididae) up an altitudinal gradient and showed that all populations had a comparatively higher metabolic rate at 45°C than at 35°C in both male and female adults.

The lack of variation in metabolic rate between species and populations is surprising, as in similar experiments involving Orthoptera, mass specific oxygen consumption was almost always elevated in high altitude populations compared to low altitude populations at the same temperature. In a study utilising one species along an altitudinal gradient, *Aeropedellus clavatus* (acrididae), Hadley and Massion (1985) tested mass specific VO_2 in Boulder, Colorado and showed that VO_2 increased with altitude, a positive correlation which they attributed to adaptation to lower temperatures at higher altitude. Likewise, individuals acclimated to the lowest temperature had higher standard metabolic rates at set temperatures than those acclimated at higher temperatures in a study conducted by Lachenicht, et al. (2010) and at both 30°C and 35°C. Massion (1983) showed a higher rate of VO_2 in montane grasshoppers (*Trimerotropis suffusa*) than lowland and sagebrush grasshoppers (*Trimerotropis pallidipennis*) by 1.86 times in males and 1.36 times in females (at 30°C) and by 1.7 times in both sexes (at 35°C).

However, one study (Ashby, 1997) did show that although populations at higher altitudes showed an increase in VO_2, but mass also increased proportionally, owing to Bergmannian size clines, resulting in no difference in mass specific VO_2 seen between the populations (Table 4.4). In the New Zealand tree weta studied here, there is a significant size difference between the two species and small intraspecific variation. The larger size of *H. crassidens* adults does allow an increased total VO_2, compared to adult *H. thoracica*, but this is small and unlikely to result in a competitive advantage.

4.6 Conclusions

The two tree weta species on Mt. Taranaki do not differ in mass specific VO_2, and neither species varies significantly with altitude, as seen in other orthopteran studies. Instead, the only significant difference among treatment groups was between temperatures. Although neither the Mt Taranaki population nor *Hemideina crassidens* showed higher mass specific VO_2 than their counterparts we cannot rule out the possibility that competitive exclusion prevents extensive overlap of these two species on Mt Taranaki. Other physiological or behavioural adaptations to high-altitude might confer an advantage to *H. crassidens* over *H. thoracica*. For example, freeze tolerance or timing of development or activity or digestive efficiency might differ between the two species allowing dominance of *H. crassidens* at high altitude.

5 Conclusions

An improved knowledge of the distribution of North Island *Hemideina* sp has increased our understanding of the ecologies of these species. This is in part due to a greater abundance of roost boxes being dispensed but, mostly due to hand collections of tree weta during countless hours of fieldwork. *Hemideina crassidens* is now found further north than previously recorded (although restricted to frost-flats) but overlap with *Hemideina thoracica* is still restricted to relatively small areas. Significant differences in mean and average temperature experienced by *Hemideina crassidens* and *Hemideina thoracica* were observed and these may be key to understanding competitive outcomes. Size variation within *H. thoracica* suggests there may be a link between temperature and 'degree days' in determination of their respective ranges.

In the 16 years since the distributions of tree weta on Mt Taranaki were first mapped, *Hemideina thoracica* has increased its altitudinal threshold on Mt Taranaki whilst displacing *H. crassidens*. However, without fine scale environmental data on the mountain, we can only assume that this is in response to an increase in temperature, therefore, further studies should concentrate on more detailed mapping of the environmental conditions as they change with altitude and season on Mt Taranaki.

Neither measurement of size (mass or tibia) appears to be better than the other for determination of age/instar; however, a combination of the two can result in accurate estimation of age when species is known. And whilst *Hemideina crassidens* and *H. thoracica* are easily distinguished in the field by colouration and abdominal and pronotal markings, I have shown for the first time that *H. crassidens* on average attains a greater weight than *H. thoracica* but *H. thoracica* is the 'longer legged' of the two species. Further morphometric studies are likely to show other size dimorphisms between the species, in particular with regards to sexually mature males and their mandibles. More in depth morphometric studies of 9th instar maturing males would be beneficial to establish at what point in development an individual insect determines its instar at maturity.

It was surprising that the two species do not differ in growth rate under constant conditions. Instead, variation in growth rate is attributed to a combination of location and temperature;

and sex and species. Weta from higher altitude (for both species) grow faster than conspecifics from low altitude. The difference was greater at the higher temperature, possibly because a mountainous environment undergoes greater seasonal fluctuations in temperature. Interpretation of this result requires further information about the natural temperature range experienced by tree weta in the North Island. Sex and species had minor but significant effects on growth rate. The major disparity between populations in their growth rate suggests the same environmental pressures had led to independent but similar adaptation of Mt Taranaki tree weta.

Surprisingly, this study found no differences in oxygen consumption between the Palmerston North and Mt Taranaki populations, or between species. This suggests that there is no metabolic adaptation in Mt Taranaki tree weta despite their increased rate of growth that resulted in larger adults compared to low-altitude adults. Thus this study can rule out a role for differential metabolic activity as an explanation for the distribution of *H. crassidens* on the top of Mt Taranaki and exclusion by *H. thoracica* lower on the mountain. The high altitude *H. crassidens* are isolated from low altitude conspecifics and exposure to a colder climate, but the mountain *H. thoracica* were not isolated just a few 100 years ago (Wilmshurst, Higham, Allen, Johns, & Phillips, 2004). It may be that both species and both populations function 'normally' at the 6°C and 14°C temperatures exposed to in this study and that a greater range of temperatures is needed to show significant differences in oxygen consumption. It is reassuring to see that tree weta did show a higher oxygen consumption rate at 14°C than at 6°C which leads me to predict that there will be a greater disparity between populations at more extreme temperatures.

If variation in metabolic rate does not explain the growth rate variation detected here, then some other adaptation involving perhaps digestion or activity must be involved. Future work comparing low and high altitude populations of both *Hemideina crassidens* and *Hemideina thoracica* might fruitfully focus on quantity eaten and digestive efficiency.

6 Appendix

6.1 Growth Rate Analyses

Table 6.1 Standard errors for growth rate (tibia)

	Pn 14	Ts 14	Pn 9	Ts 9
EM Hc	0.0031	NA	0.0066	NA
EM Ht	0.0051	NA	NA	0.0034
F Hc	0.0227	0.011	0.0154	NA
F Ht	0.0039	NA	0.0053	0.0328
M Hc	0.004	0.024	0.0167	0.0058
M Ht	0.0088	0.019	0.01	0.0047

Table 6.2 Full factorial model for growth rate (tibia).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Temperature	1	0.012215	0.012215	6.5171	0.01175
Location	1	0.04617	0.04617	24.6324	1.97×10^{-6}
Sex	2	0.0098	0.0049	2.6142	0.07678
Species	1	0.00008	0.00008	0.0427	0.83652
Temp:Location	1	0.013138	0.013138	7.0095	0.00903
Temp:Sex	2	0.003159	0.001579	0.8426	0.43274
Location:Sex	2	0.000971	0.000486	0.2591	0.77211
Temp:Species	1	0.001729	0.001729	0.9222	0.33853
Location:Species	1	0.000503	0.000503	0.2684	0.60523
Sex:Species	2	0.011024	0.005512	2.9407	0.05608
Temp:Location:Sex	1	0.002589	0.002589	1.3811	0.2419
Temp:Location:Species	1	0.005775	0.005775	3.0812	0.08137
Temp:Sex:Species	1	0.00032	0.00032	0.171	0.67989
Location:Sex:Species	1	0.000269	0.000269	0.1435	0.70543
Residuals	141	0.264285	0.001874		

Table 6.3 Means for growth rate (mass).

	Pn 14	Ts 14	Pn 9	Ts 9
EM Hc	0.0544	NA	0.0276	0.039
EM Ht	0.01	NA	NA	NA
F Hc	0.0227	0.079	0.0241	NA
F Ht	0.0469	0.063	0.0385	0.076
M Hc	0.0252	0.109	0.0153	0.021
M Ht	0.0034	0.071	0.0056	0.048

Table 6.4 Standard errors for growth rate (mass)

	Pn 14	Ts 14	Pn 9	Ts 9
EM Hc	0.0031	NA	0.0066	0.0034
EM Ht	0.0051	NA	NA	NA
F Hc	0.0227	0.011	0.0154	NA
F Ht	0.0039	NA	0.0053	0.0328
M Hc	0.004	0.024	0.0167	0.0058
M Ht	0.0088	0.019	0.01	0.0047

Table 6.5 Full factorial model for growth rate (mass)

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Temp	1	0.012215	0.012215	6.467	0.012068
Location	1	0.04617	0.04617	24.4431	2.14×10^{-6}
Sex	2	0.0098	0.0049	2.5941	0.078278
Species	1	0.000037	0.000037	0.0194	0.88931
Temp:Location	1	0.013122	0.013122	6.9472	0.009335
Temp:Sex	2	0.003216	0.001608	0.8513	0.429048
Location:Sex	2	0.001018	0.000509	0.2695	0.764121
Temp:Species	1	0.001085	0.001085	0.5743	0.449837
Location:Species	1	0.000113	0.000113	0.0596	0.807408
Sex:Species	2	0.011536	0.005768	3.0536	0.050321
Temp:Location:Sex	1	0.003158	0.003158	1.6717	0.198141
Temp:Location:Species	1	0.003637	0.003637	1.9256	0.167432
Temp:Sex:Species	1	0.00032	0.00032	0.1696	0.681059
Location:Sex:Species	1	0.000269	0.000269	0.1424	0.706515
Residuals	141	0.266332	0.001889		

Table 6.6 Reduced model for growth rate (mass) of tree weta.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Temperature	1	0.01222	0.01222	6.603	0.01115
Population	1	0.04617	0.04617	24.957	1.60×10^{6}
Sex	2	0.0098	0.0049	2.6486	0.07404
Species	1	0.00008	0.00008	0.0433	0.83544
Temp:Pop	1	0.01314	0.01314	7.1019	0.00854
Sex:Species	2	0.01128	0.00564	3.0477	0.0504
Residuals	151	0.27935	0.00185		

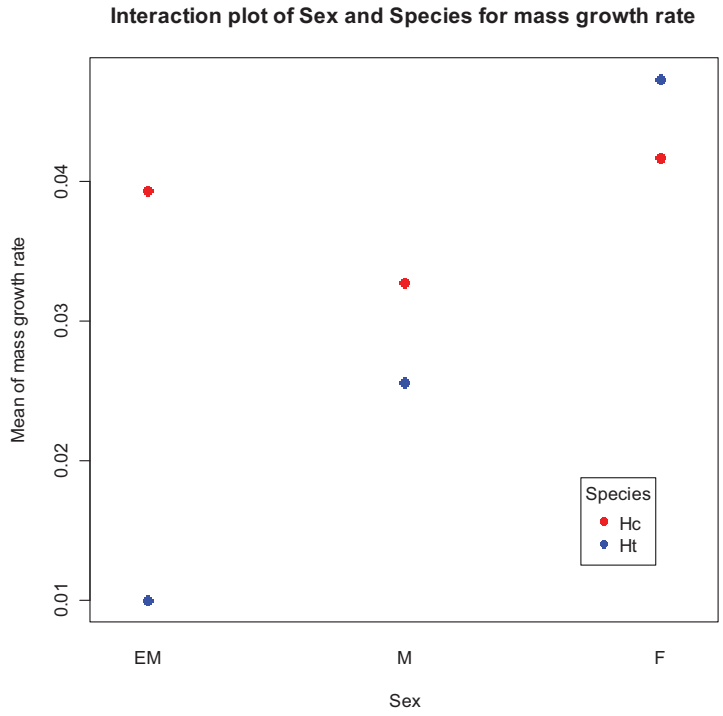


Figure 6.1 Interaction plot for mass growth showing the dependence of temperature and sex.

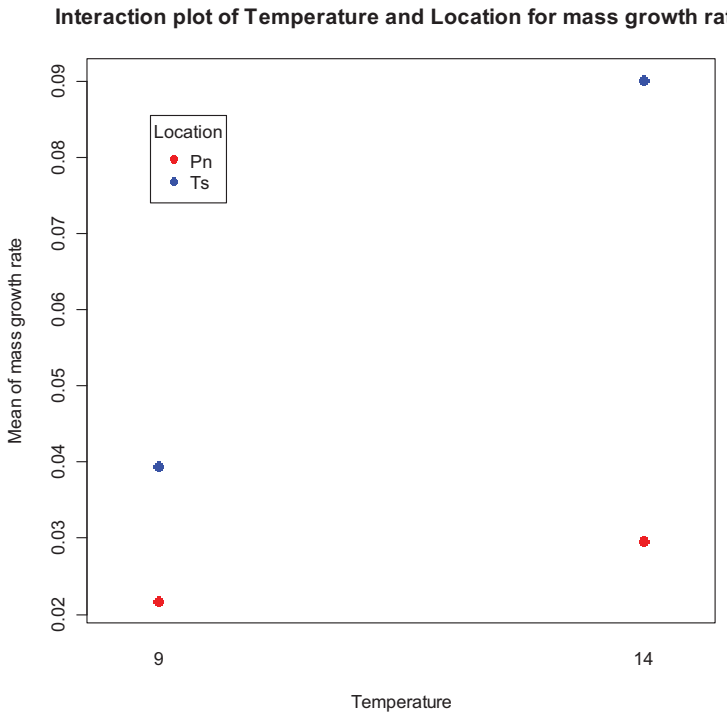


Figure 6.2 Interaction plot for mass growth showing the dependence of temperature and altitude.

6.2 Weta tested for oxygen consumption

				Date Tested	
Weta	**Sex**	**Species**	**Population**	**6 degrees**	**14 degrees**
HcPn-127	F	*H. crassidens*	Palmerston North	4.11.10	13.09.10
HcPn-128	F	*H. crassidens*	Palmerston North	2.11.10	13.09.10
HcPn-133	M	*H. crassidens*	Palmerston North	7.01.11	29.10.10
HcPn-134	M	*H. crassidens*	Palmerston North	6.11.10	27.09.10
HcPn-180	F	*H. crassidens*	Palmerston North	14.01.11	10.09.10
HcPn-185	F	*H. crassidens*	Palmerston North	5.11.10	10.09.10
HcPn-226	M	*H. crassidens*	Palmerston North	5.11.10	29.09.10
HcPn-311	M	*H. crassidens*	Palmerston North	9.11.10	18.10.10
HcPn-312	M	*H. crassidens*	Palmerston North	3.11.10	04.10.10
HcPn-334	M	*H. crassidens*	Palmerston North	10.12.10	29.10.10
HcPn-337	M	*H. crassidens*	Palmerston North	19.01.11	18.10.10
HcPn-487	M	*H. crassidens*	Palmerston North		08.10.10
HcPn-491	M	*H. crassidens*	Palmerston North	3.11.10	04.10.10
HcPn-492	F	*H. crassidens*	Palmerston North	21.01.11	11.10.10
HcPn-493	F	*H. crassidens*	Palmerston North	8.11.10	13.10.10
HcPn-496	F	*H. crassidens*	Palmerston North	4.11.10	13.10.10
HcPn-497	M	*H. crassidens*	Palmerston North		11.10.10
HcPn-498	M	*H. crassidens*	Palmerston North	25.01.11	27.10.10
HcTs-394	F	*H. crassidens*	Mt Taranaki		28.09.10
HcTs-395	M	*H. crassidens*	Mt Taranaki		18.06.10
HcTs-396	F	*H. crassidens*	Mt Taranaki	13.01.11	15.10.10
HcTs-398	M	*H. crassidens*	Mt Taranaki		22.10.10
HcTs-399	M	*H. crassidens*	Mt Taranaki		22.06.10
HcTs-431	M	*H. crassidens*	Mt Taranaki	18.11.10	27.10.10
HcTs-434	F	*H. crassidens*	Mt Taranaki	17.11.10	28.10.10
HcTs-435	F	*H. crassidens*	Mt Taranaki	13.12.10	
HcTs-436	F	*H. crassidens*	Mt Taranaki	1.11.10	20.09.10
HcTs-437	F	*H. crassidens*	Mt Taranaki	11.01.11	22.10.10
HcTs-439	F	*H. crassidens*	Mt Taranaki	1.11.10	20.09.11
HcTs-441	M	*H. crassidens*	Mt Taranaki	6.01.11	15.10.10
HcTs-442	M	*H. crassidens*	Mt Taranaki	4.11.10	29.09.10
HcTs-448	F	*H. crassidens*	Mt Taranaki	10.01.11	19.10.10

HcTs-480	M	*H. crassidens*	Mt Taranaki	24.01.11	
HtPn-130	F	*H. thoracica*	Palmerston North		06.09.10
HtPn-143	F	*H. thoracica*	Palmerston North	10.11.10	23.09.10
HtPn-146	F	*H. thoracica*	Palmerston North	14.12.10	24.09.10
HtPn-149	F	*H. thoracica*	Palmerston North		06.09.10
HtPn-178	M	*H. thoracica*	Palmerston North	18.01.11	07.09.10
HtPn-192	F	*H. thoracica*	Palmerston North	12.01.11	21.10.10
HtPn-193	F	*H. thoracica*	Palmerston North	17.01.11	14.09.10
HtPn-200	F	*H. thoracica*	Palmerston North	31.01.11	14.09.10
HtPn-204	M	*H. thoracica*	Palmerston North		12.10.10
HtPn-206	M	*H. thoracica*	Palmerston North	3.11.10	05.10.10
HtPn-209	F	*H. thoracica*	Palmerston North	16.12.10	07.09.10
HtPn-211	M	*H. thoracica*	Palmerston North		12.10.10
HtPn-257	F	*H. thoracica*	Palmerston North	8.12.10	15.09.10
HtPn-258	F	*H. thoracica*	Palmerston North	8.11.10	14.10.10
HtPn-259	F	*H. thoracica*	Palmerston North	28.01.11	15.09.10
HtPn-260	F	*H. thoracica*	Palmerston North	01.02.11	14.10.10
HtPn-292	F	*H. thoracica*	Palmerston North		16.09.10
HtPn-348	F	*H. thoracica*	Palmerston North		28.09.10
HtTn-466	F	*H. thoracica*	Mt Taranaki		21.09.10
HtTs-443	M	*H. thoracica*	Mt Taranaki	30.11.10	28.20.20
HtTs-444	M	*H. thoracica*	Mt Taranaki		22.09.10
HtTs-445	M	*H. thoracica*	Mt Taranaki	29.11.10	20.10.10
HtTs-446	M	*H. thoracica*	Mt Taranaki	15.11.10	05.10.10
HtTs-447	F	*H. thoracica*	Mt Taranaki	16.11.10	21.10.10
HtTs-449	M	*H. thoracica*	Mt Taranaki		21.09.10
HtTs-484	F	*H. thoracica*	Mt Taranaki	13.12.10	
HtWai-287	F	*H. thoracica*	Palmerston North		17.09.10
HtWai-290	F	*H. thoracica*	Palmerston North	9.12.10	27.09.10
HtWai-292	F	*H. thoracica*	Palmerston North	3.12.10	

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